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Editorial

GRAZING BEHAVIOUR

The first issues of this Journal have contained several of the papers presented at the Association's symposium on grazing behaviour, held in London over two years ago, and the remaining contributions are due to appear in forthcoming numbers. While the unavoidable delay in publication is regretted, it is refreshing to renew acquaintance with this important subject, clearly an "applied" aspect of the Association's work that requires much further study.

Modern studies of grazing behaviour may perhaps be said to have begun with the observations of Cory, followed during the 1930's by the contributions of Johnstone-Wallace and his colleagues. To Johnstone-Wallace certainly we owe much of the current interest in the subject, now under active investigation at a variety of centres in this country and elsewhere, and the resuscitation of the data put on record by Anderson nearly two centuries ago. But for their style, the descriptions furnished by Anderson of rotational grazing might come from a modern text-book. Since 1944, when a further paper by Johnstone-Wallace was read before a joint meeting of the Association with the British Society of Animal Production, we have seen very considerable additions to basal knowledge and, equally important, the beginnings of critical interpretation, including those made by Tribe and Holmes. The behaviour patterns of a domesticated animal are not always conducive to optimal health status combined with productivity unless suitably controlled by man. The food preferences of a sheep may be compatible with survival on the mountain, but disastrous if allowed free rein on the lowland farm. Behaviour studies emphasize, therefore, the continued need for supervision and regulation of grazing, but they nevertheless provide additional proof, if that were necessary, of understanding the animal itself more fully if health and production are to be at their best. As Dr. John Hammond has said, the study of animal behaviour will have a great influence in making a science of what is now known as the stockman's art.

Obituary

JAMES THOMAS GRIFFITHS EDWARDS

D.Sc.(LOND.), M.R.C.V.S.

1889 - 1952

The distinguished life and work of "J.T.", as he was affectionately known to his many friends, have been reviewed in detail in our contemporary, *The British Veterinary Journal* (Vol. 109, 1953, pp. 76-86), in a memoir to which is appended a list of his published writings. It remains only for us to record with appreciation the enthusiastic part that he played in furthering the interests of animal behaviour. Some fifteen years ago he befriended and subsequently gave a home to the late Dr. A. Loeser and there is little doubt that this contact stimulated his already keen interest in the subject. Edwards did everything that he could to encourage

the veterinary profession to take up behaviour studies, and when called upon to advise the Egyptian authorities his firm recommendation was to the effect that animal behaviour should form an integral part of the veterinary curriculum.

Edwards helped materially to strengthen this Association, on the Council of which he served for a number of years. He was responsible for finding members, speakers and authors, and it was primarily his suggestion that led to the arrangement whereby this *Journal* was launched. The veterinary profession and animal behaviourists have lost a friend who did more than anybody else to bring them together.

Some Behaviour Problems in Common Laboratory Animals*

By W. LANE-PETTER

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It is a fallacy which scarcely needs emphasis among biologists to regard experimental animals as inanimate reagents, and to make no allowance for the physical responses of these animals to environmental factors which are not immediately physical, but exert their effect through altered behaviour. According to this fallacy, if the animal does not grow, the diet is at fault: if it does not breed, there is an endocrine disorder: if it will not keep still while it is being inoculated, it must be forcibly restrained. Such paralogism is not possible if the animal is regarded as having its own innate behaviour pattern, representing one of the links between the physical environment and the physical response of the animal.

In nearly every case laboratory animals are required to show a high degree of uniformity, not only in a single batch—say a litter group—in one laboratory, but in a known strain in different laboratories and at different times. I have dealt elsewhere† with some aspects of this need for uniformity and how it may be pursued, but now I want to draw attention to one or two ways in which the study of the animal's behaviour can contribute to the total sum of uniformity in a group of animals whose breeding and physical environment are already closely regulated.

Mice, which comprise, numerically, some four fifths of all vertebrate animals used in laboratories in this country, may be either docile and easily handled, or lively, intractable, fugitive and liable to bite. One strain may have been bred for the character, *inter alia*, of handleability: another, selected for other characteristics and without regard to easy handling, may prove extremely troublesome. In any selection programme, therefore, it would seem desirable, not to say essential, to breed for docility; yet this point is often not taken into account.

* Presented at symposium on Domestication, held at the Zoological Society, London, on 25th February, 1953.

† *Laboratory Practice*, 1, 30.

Moreover, one may suspect that a strain which reacts vigorously in its behaviour to normal handling may also show other physical responses related to the particular kind of handling required by the experiment rather than the specific test procedure utilised.

But of course no amount of selection will produce an animal which responds to none other than the grosser factors in its environment, such as the nature of its diet, the temperature of the animal room and so on. The way it is looked after will always be important, and the less effect of easily defined factors in its daily and weekly routine will always be demonstrable in such objective observations as growth rate, breeding performance, and infant mortality. The personal element, in other words, is always to be reckoned with, and the skill of the technician attending to the routine care of the animal is likely to affect in greater or less degree the experiments for which the animal is being bred. Recognition of the importance of this personal element is no new thing—indeed, it is quite fashionable today—but it is not the only imponderable which can produce marked physical effects on animals.

Last year my regular animal technician took two weeks holiday. Part of her duties was the routine care of a small colony of guinea pigs, comprising 26 adult and a variable number of young. During the previous 5½ months, since the establishment of this particular colony, there had been no deaths at all, but in the fortnight when another technician, equally competent and conscientious, was in charge four adult guinea pigs died. We never discovered the cause of death, for *post mortem*, including bacteriological, examination did not reveal anything abnormal. No doubt a fuller investigation would have uncovered the reason for their losses, but this was not done, for with the return of the regular technician, deaths ceased.

At Hampstead we have had occasion to compare the rate of growth of weanling mice offered various diets. All the mice are kept in sheet metal boxes, ventilated through the lid, and supplied with fine peat moss bedding. Water is given by bottle, and food is placed in a wire basket, in accordance with standard practice. All the mice are kept in the same small room, and parallel observations are made in boxes on the same shelf.

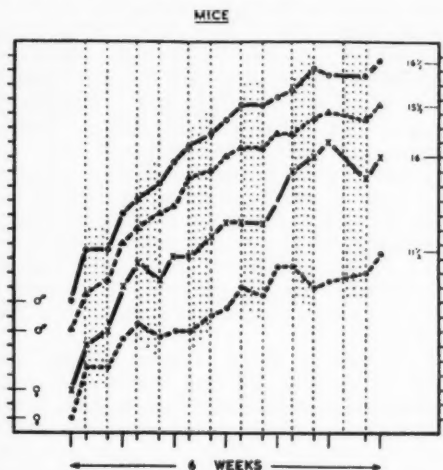


Fig. 1

Fig. 1 shows the growth rate of individual mice over a period of six weeks. The shaded portions are the weekends—Friday, Saturday and Sunday—and the unshaded portions the other four days of the week. The tendency for growth to slow down, to stop, or even to go into reverse, over the weekends is obvious. Weighings were done on Monday and Friday mornings (and sometimes on Wednesdays as well).

Fig. 2 shows a similar record of growth over a period of six weeks and three days. In this case weighings were done on Monday mornings and Thursday afternoons.

Measurements of food intake show no corresponding contrast between weekdays and weekends; they are not significantly different for any day or days of the week. The temperature of the mouse room has been checked by thermographic records, and the variation is slight and inconstant—it depends much more on the outside temperature, the diligence of the

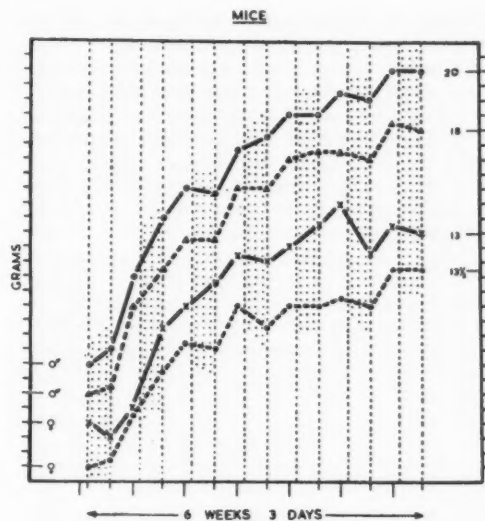


Fig. 2

stokers, and other factors which do not show a weekly rhythm. Yet the average gain in weight per mouse per day for the days Monday-Thursday is three, four or more times greater than it is for the days Friday, Saturday and Sunday as is shown in the table.

Average Gain per Mouse per day (GM.)

	WEEK	WEEK-END
I		
♂	.565	.171
♀	.630	.039
II		
♂	.622	.153
♀	.520	.122

Although the figures given apply only to eight mice they are representative of a much larger number for which records have been kept.

I do not know the reason for this weekend slowing down of growth, but will offer one rash observation. If one visits the animal house in the evening, and stands outside the door of the mouse room, the commotion going on inside is considerable, much greater than during the day. This greater commotion is also easily discernible on Sundays. If one enters the room, the commotion dies down. Quite apart from the

24-hour rhythm of a nocturnal animal like the mouse it seems that the presence of human activity depresses murine activity, so that the mice keep quiet and grow fat. Absence of human activity is attended by increased murine activity; the mice eat as much as usual, but work it off. I have not made any measurements of activity on different days, because I have not any suitable instruments. It would be interesting, however, to do so.

These observations are not particularly original, but they serve to introduce the next topic; one which is of urgent interest to all users of laboratory animals. This is the problem of cage size and design which, it seems to me, can only be satisfactorily solved by properly conducted studies of behaviour. Cages of certain sizes are in common use for many different species of laboratory animals, but no general agreement exists about minimum and optimum sizes and patterns. Attempts to find the answers through measurements of growth rates, breeding performances and the like are only partially successful because they ignore the study of the animals' behaviour. I have postulated that "there is a critical size below which the animal will not maintain health, although it may succeed in remaining alive for a considerable period. There is probably another critical size above which it is necessary to go if the animal is to exhibit its optimum growth, breeding performance and instinctive pattern." It is likely that for recently domesticated species this second critical size is coterminous with the animal's natural habitat, but the same is not necessarily true of the common laboratory rodents which have sheltered under the umbrella of domestication for so long. If the hypothesis of a physical minimum, and an optimum size be accepted for the time being, it may be said that the majority of laboratory animals are confined in cages of intermediate size. Examination of the practice prevailing in a number of scientific institutions where animals—most laboratory rodents—are kept under good conditions makes it possible to devise a formula for cage size. Such a formula is of necessity empirical, but perhaps it will help until a proper study of this problem replaces it with something more solidly founded on reason rather than custom.

For animals to be confined for periods of days or weeks, the size of the cage should be

$$A = n(3W + 5\sqrt{W}) \text{ or } A' = n(0.7W' + 6\sqrt{W'})$$

where A = floor area in sq. ins. (A' in sq. cm.), W = weight of individual animals in oz. (W' in gm.), and n the number of animals in the cage. No dimension of the cage should be less than the length of the animal, less its tail. It follows from the above that the grouping of animals together does not save total space, whatever other advantages it may have.

As an illustration of the fact that this problem of space allocation cannot be solved merely by observation of the grosser features, such as growth rate, infant mortality and the like, may be cited the findings of three independent breeders of guinea pigs, two attached to scientific institutions, and the third a commercial breeder. All breed guinea pigs in colonies containing a boar and a number of sows. The first has found that the floor space required is 1.7 sq. ft. per sow; crowding beyond this point leads to a sharp rise in infant mortality. The second finds 1 sq. ft. sufficient, while the third has cautiously but successfully reduced the figure to 0.6 sq. ft. per sow—12 sows and a boar, plus their progeny, in a pen 3 ft. x 2 ft. 6 ins.

Or again, a rabbit breeder whose does were casting litters ranging from 8 to 12, with negligible losses from birth to weaning, found that the rate of growth of the young was greater when the hutch was 20 sq. ft. in area than when it was 12 sq. ft. But another breeder found that the reverse is true of his rabbits; he gets more rapid growth when the hutch is so small that the young when near weaning age have little more room than is necessary for them to turn round and get at the food and water.

Here, then, is a case, and urgent one, for study of the animal as a whole, and not just as something which puts on weight or produces so many young at intervals. To keep an animal in a cage will inevitably modify its behaviour in several ways, not always to the disadvantage of the animal. Certain types or sizes of cage may affect the animal adversely and offend both humanitarian considerations and also scientific requirements. This is no less true of the recently domesticated animal than of the laboratory rat, mouse, guinea pig or rabbit which has been bred under laboratory conditions for countless generations. An unnecessarily large cage will take up so much room in the animal house that the already high cost of maintenance will be fruitlessly multiplied. A cage of dimensions smaller than those dictated by custom, conjecture, anthropomorphic misconception or

the above empirical formula may not necessarily interfere with the well-being of its inmate. It is quite unjustifiable to assume that the bigger the cage, the better for the animal. Similarly, the other details of the animal's confinement such as shape, structure and materials of the cage, and the design of feeding and drinking utensils, merits rational consideration, rather than preconceived assumption.

There is a great need for some real information on this subject. Cages are expensive items of equipment and there is such a multiplicity of design that standardisation remains unattainable in the absence of precise knowledge: yet standardisation of, say, mouse boxes, would reduce the cost considerably.

The common laboratory rodents are second only to the cats, dogs and farm livestock in the degree to which they have been domesticated. They are essential allies in innumerable fields of scientific investigation, and are certain to remain so. Some of them have been the subject of behaviour studies. It is likely that if the rat and the mouse, the guinea pig and (though no longer a rodent) the rabbit became more the *object* of such studies, much light would be thrown on how best to breed, rear and maintain them.

The outcome would be a better biological reagent, which would please the investigator; a more contented animal; and a satisfying application of scientific knowledge and method.

Bait Shyness, a Study in Rat Behaviour

By JULIAN RZÓSKA

University College, Khartoum

Formerly of the Bureau of Animal Population, University of Oxford

The behaviour of rats, extensively studied from the theoretical point of view, is an important factor in rodent control. In traditional as well as practical and scientific experience (e.g. Hamilton 1936, Doty 1938, Dopmeyer 1936), the avoidance of poison bait by rats has been frequently mentioned, but little attempt has been made to analyse this phenomenon more closely.

The present paper contains a summary of a series of laboratory experiments on this subject and an attempt to draw conclusions. This work was carried out within the framework of war-time research on rodent control at the Bureau of Animal Population, Oxford, in the years 1941-1946.*

MATERIALS AND METHODS

Our evidence is based on five main sets of experiments with 162 white rats, in which a succession of baits of arsenic and barium carbonate was employed. Several minor tests with tame white and wild brown rats are also

The detailed description of the experiments and the tabulated evidence is deposited at the Bureau of Animal Population, Oxford.

GENERAL RESULTS

We shall try to analyse and compare the various findings of our experiments and fit them together into a comprehensive picture. For this reason the behaviour of the rats will be traced from the attitude to an initial poison bait through successive manifestations of bait approach to the finer and more complex aspects of behaviour.

1. Initial Acceptance

Under the conditions of experiments, white rats with no previous experience of poison bait mostly accepted a first poison bait, and a majority consumed it entirely. In each test there were a few rats which either refused the bait, or, more commonly, ate it only partly; their numbers are shown in Table 1.

Table 1

Exp. 1	With Arsenic (♀ + ♂)	Refused	0/20	Accepted Partially	3/20 (15%)
2a	" " (♀)	"	0/12	" "	2/12 (16.6%)
2b	" " (♀)	"	0/12	" "	Negligible Amounts
5	" red squill (♂)	"	2/55 (3.6%)	" "	3/55 (5.4%)
6	" bar. carbon. (♂)	"	4/40 (10%)	" "	3/40 (7.5%)
	" " " (♀)	"	1/39 (2.5%)	" "	3/39 (7.6%)

included. Finally the results of a test on memory of squill baits, done by the late R. M. Ranson, have been reanalysed.

The general procedure in most of the experiments was to treat survivors of initial poison baits with successive doses of the same or a different poison in the same or a different food base. Each animal was kept in a separate cage and provided with normal food and water in between the poison tests. These were usually preceded by 24 hours starvation. All white rats used, with few exceptions, were medium sized (150-300 g.) and at least 5 months old. They came from pure white inbred Wistar stock.

* The main part of this work is in the process of publication.

The refusal of a bait without previous experience is rare and may be due to minute nibbling and subsequent rejection of the baits; it should be noted that red squill is bitter and barium carbonate baits harden quickly. A main factor however is "individual behaviour," which will be discussed later.

2. Behaviour towards Successive Baits

The ready acceptance of the initial bait by the majority of rats was not repeated in successive trials with the survivors. A change of behaviour took place and expressed itself in a range of attitudes from strict refusal through various degrees of hesitation to in a few cases repeated acceptance. The attitude varied

according to the kind of poison bait offered initially and in succession. In its stricter manifestation this "bait shyness" may be defined as a cautious attitude towards food (and poison bait) experienced previously with harmful effects.

Besides this attitude, clearly directed against a special bait, there was in some cases a change of behaviour even towards plain food. This is illustrated by the cautious approach to plain bread paste by male rats after an experience with an entirely different poison bait a week before. During the first hour this food was only nibbled in spite of starvation. This suggests that experience with poison baits might create a general state of higher attention or alertness, similar to that recorded in certain situations in experiments by animal psychologists (e.g. Maier and Schneirla, 1935; 312, 421). It is important to distinguish these manifestations of a change of behaviour from a refusal to eat due to illness.

3. The Various Forms of Bait Shyness

If the results of the experiments are compared and grouped, the following main cases are clearly distinguishable:

Refusal of Identical Poison Bait

In all experiments successive identical poison baits were mostly refused by the majority and always by at least some of the animals.

Successive baits of arsenic in bread paste were strictly refused by all animals after 46 days, and two weeks later by 11 out of 12 animals. The same rats also met three successive baits of arsenic and oiled wheat grains; an increasing number of rats refused, the remainder took only samples. In another experiment all animals strictly refused an identical poison bait, whereas they accepted the same poison in an unfamiliar base. In the red squill test a general sharp decrease of take was noticeable after the consumption of the initial poison bait; the strength of refusal varied individually. Successive barium carbonate baits in bread paste were accepted by a sharply decreasing number of rats. Arsenic on kibbled wheat was refused when offered for 9 days in succession to three brown rats with an experience of this poison bait, and arsenic on whole wheat was also refused. Five other brown rats also refused a familiar poison bait.

Shyness towards successive identical poison baits is evident in all these cases. There are variations depending upon the nature of the base, the poison and individual behaviour, and some animals accepted the same bait again; these exceptions will be discussed later.

Refusal of a New Poison in Experienced Base

If the same base was used again with a new poison, the tested animals usually refused it.

Four days after taking barium carbonate in bread paste with no outward sign of illness, six out of seven rats refused arsenic in the same food. This also happened with five out of six animals, which met arsenic in either of two bases in which they had eaten barium carbonate a week before. One of the five rats nibbled some of the oiled wheat grains, which was one of the bases. Similarly, barium carbonate in bread paste was uniformly refused by five rats which had survived two doses of coarse arsenic in the same base. The complete refusal by 10 rats of an initial bait of barium carbonate in bread paste was the more interesting as its reason was unknown, until the discovery that they had had red squill in that base a month before. In the series of tests on barium carbonate four out of six rats later refused arsenic in the same base.

In the early phases of our investigations such cases were interpreted as "cross prejudice," an avoidance of one poison on the basis of harmful experience with another, but this was proved to be a wrong conclusion.

Acceptance of Experienced Poison in New Base

A poison previously experienced was on the whole accepted when offered in a new base.

After seven days a second dose of barium carbonate in a different base was consumed entirely by four out of five female rats and the fifth ate most of it. Male rats were much more reluctant. In the same experiment 12 rats given two barium carbonate and three arsenic baits within 72 days, were finally given the choice of the two previously used and a new base with arsenic. Ten of them were killed by the experienced poison in the new base. In another experiment, after two poisonings with barium carbonate and arsenic, 18 surviving rats were given a choice of two bases with arsenic. There were 16 fatal acceptances; 13 of them chose a base not previously experienced with a poison, which some of them had consumed before. Five rats accepted arsenic for the third time but in a new base in a further test.

In all these cases a majority did not recognise a previously experienced poison in a new base. There were some exceptions; some individuals refused, some ate only part of the baits.

Acceptance of a New Poison in a New Base

A new poison in a new base was accepted by all animals in two tests made.

After taking barium carbonate, six rats met arsenic in a base not harmfully experienced. All accepted, five ate the full bait. In the red squill experiment the survivors of 23 squill attempts accepted a fatal dose of arsenic in bread paste, after a day's prebaiting with that base in plain form.

This closes the range of possibilities of changing poison and base.

4. The Role of the Base and the Poison in Bait Shyness

Four main results were obtained, whenever experimental animals were confronted with a particular combination of poison and base.

- (a) An identical poison bait was refused on successive occasions.
- (b) A new poison in a base harmfully experienced was rejected.
- (c) An experienced poison in a new base was accepted.
- (d) A new poison in a new base was accepted.

There were deviations and exceptions to these rules, which will be discussed later. But the results obtained with the majority of rats clearly suggest the important role played by the base. A food consumed together with a sufficiently powerful poison was recognised when it was met next time. It was approached cautiously and rejected if poisoned.

Very striking behaviour was shown by the majority of rats in a choice test given after previous experiences. Thirteen out of 16 rats accepting a bait chose an experienced poison in whichever one of two bases was not previously connected with poison. It is of interest to note that the experimenter predicted for each individual, which bait it would chose. The remaining animals fall under rules to be mentioned later.

The poison makes the animal ill or uncomfortable, but mostly it appeared to be recognised through the medium of the base and not for itself. Substantial evidence was obtained when "fresh" animals participated in poison tests together with "experienced" ones.

In a choice test with arsenic in three bases, experienced rats accepted the new base in preference to the other two, known to them, whereas the fresh animals showed no discrimination. The same happened in another experiment; here the "fresh" animals knew both bases as plain food and according ate poison in both, whereas "experienced" rats acted strictly according to their previous varied unpleasant experience.

Apparently, then, an "association" was formed between the particular base and the illness felt when it was consumed with a poison; even if offered in a successive trial without poison it was approached with caution and rejected at first. This type of behaviour towards the food medium, base shyness, is an important characteristic of behaviour.

5. Development of Base Shyness

This change of behaviour from acceptance to refusal of a bait was studied in a series of experiments on the development of "warning symptoms," arising in the course of poison bait feeding.* These consisted in tests where rats, previously conditioned to accept food in small pieces by hand, were offered an initial calculated poison dose in a base followed by $\frac{1}{4}$ g. pieces of the plain base at five minutes in-

* See main work.

tervals. In most of these experiments the change from acceptance to refusal occurred sharply in well defined time limits, according to poison and dosage given, until illness and maybe death overwhelmed the purely psychological situation. When weak doses were given the development of bait shyness was less stringent and slower. Rats treated with such doses had several refusal reactions and renewals of take during the hours of the experiment, in short not a clear and lasting attitude. Some observations in the present work are of interest in this respect.

A strict avoidance of plain bread paste was recorded four hours after the consumption of a strong but sublethal dose of barium carbonate in that base. A weak dose of arsenic in bread paste did not create refusal in one hour; the animals still accepted the plain base, but most of them at first refused this base eight days later. This shows that a firm attitude can appear very slowly. Similarly, coarse arsenic of low toxic properties produced refusal symptoms only in two out of five animals within three hours and the plain base was eaten the following night by three out of five rats, but all of them refused it after three days.

It may be concluded that base shyness may in some cases gradually develop and establish itself more clearly, following the action of the poison.

6. Factors Controlling Development, Strength and Direction of Bait Shyness

Nature and Action of Poison

Identical sublethal baits of red squill powder and extract, barium carbonate and coarse arsenic were accepted and consumed in successive trials by some of the tested rats, though their numbers decreased. With fine arsenic only very low doses in identical bases were taken a second time, higher doses caused strict bait shyness in a majority of rats. It seems justifiable to conclude that various poisons cause shyness of different strength.

Dosage

In the tests on the onset of "warning symptoms" a direct relationship was established between dosage and time, strength and duration of the "hesitation" and "refusal" reaction of rats.

Low doses of arsenic gave no clear cut refusal; with increased concentrations shyness symptoms became clearer and finally strict. Avoidance of successive baits of red squill depended to some extent upon the initial dose consumed. The effect of dosage was clearly shown in tests on barium carbonate. Initial baits were accepted without relationship to their rising dosage; the acceptance of second baits was clearly influenced by the initial dose. The texture of a poison may influence the toxicity and therefore the effective dosage because of variations

shyness, if the base is offered as sole food for several days.

A striking example was afforded by 10 rats, which, a month after having had red squill powder in bread paste, entirely refused this base with another poison. Four days of prebaiting with bread paste broke down this shyness and a poison bait was taken, which had previously been strictly rejected. An identical case occurred in the barium carbonate test. In a further test three out of four survivors of seven poison tests accepted a lethal dose of a known poison in kibbled wheat, although whole wheat was previously taken with reluctance. In the red squill series offerings of the plain base usually used, and the same with non toxic Egyptian squill, resulted in an increased take of the next normal poison bait in the same base. This prebaiting acted here against an established caution.

On some occasions, when hunger drove the rats to feed on food which they disliked because of its previous strong poison association, they ate subnormal amounts of the disliked food for some days.

In experiment 1 plain bread paste was only tentatively accepted after a harmful experience. Rats which had the experience twice, ate much less than the others. Two striking cases were furnished by experiments on wild brown rats; for several days they ate only subnormal quantities of kibbled wheat as sole food, which they had previously experienced with arsenic. Intake doubled when whole wheat was offered.

These facts show that shyness may have been partly overcome but was still present and quantities eaten were subnormal. This confirms our assumption that harmful experience of poison bait increases the cautiousness of rats.

7. Discrimination of Poison and Plain Bait by Rats

Little is known about rats' senses and the subject is controversial. Doubtless their faculties are adequate for the requirements of their normal environment. This subject is discussed in an Appendix.

Discrimination by Senses Other Than Taste.

Without deciding which of the senses was responsible for the outcome, two cases of discrimination of poison bait in our experiments may be noted.

In a successive poison trial with five per cent arsenic in oiled wheat, no animal ate the full amount of 25 grains; the take was checked but the poisoned grain was left in the cages and it became mixed with the plain oats given as food. After five days the oats had been eaten by almost all rats whereas there was little change in the number of wheat grains. This is a clear distinction of two similar foods. Three brown rats ignored kibbled wheat with arsenic and for nine successive days invariably chose plain kibbled wheat, although the positions of both were constantly changed. This case of discrimination was complicated by the fact that the rats also disliked the

plain food since it had been used as a poison base. Maybe the peculiar smell which is supposed to be given off by wet starch in contact with arsenic was a guidance and aversion to the plain food was overcome by hunger.

In the above cases poisoned food was discriminated by senses other than taste. When one observes white and especially brown rats the display of sniffing and smelling is always very pronounced, especially in new situations.

Discrimination by Taste and Sampling

In most of our tests the differences between the behaviour of experienced and inexperienced animals was merely recorded. But on some occasions the course of events was followed more closely. The approach of experienced rats to known plain bases was cautious; for hours no take was noticed, but after 24 hours the suspected food was found to have been consumed, undoubtedly under pressure of hunger. Inexperienced rats consumed the particular food at once. If the suspected base was offered later with a poison, experienced animals again approached it cautiously, but after a first encounter and a limited sampling consumption, there was no further take. The cautious testing, approach of experienced animals produces then a quite different outcome if plain or poisoned food is encountered. In the case of plain food, if hunger was strong enough to break down shyness, the rats at first sampled the food reluctantly and then, with no symptoms of discomfort arising, ended with a total consumption. With poison bait either memory was stronger or a feeling of even slight discomfort prevented further feeding.

An incidental observation throws light on this important point. Two white rats left from an experiment a month before, were offered a known plain base. They began to eat, then slowed down, stopped chewing and sat immobile, finally dropping the bait. It is probable that, during chewing, the memory of the particular food was revived. Apparently the visual and olfactory memory was not strong enough to prevent the initial feeding but the gustatory memory was decisive. Similar observations were made during experiments with the poison alpha-naphthylthiourea.

No further observations on the above animals were made. It may be that with increasing hunger they would have begun feeding again, as described previously. In most of our main experiments this first tentative phase of approach remained unobserved, and the main interest was centred on the final outcome. In one of our tests there was a gradual conversion through sample take to

full acceptance of a plain base once harmfully experienced, undoubtedly by discrimination of its harmless nature. In the red squill series the plain base, offered in between the normal successive squill baits, was completely eaten in 24 hours. Also non-toxic Egyptian squill mixed with the base was consumed completely by eight and partly by three out of 17 animals. In contrast, not a single rat ate the next, toxic, bait completely though there was, after both Egyptian squill and plain base offerings, a marked rise in sampling of the next toxic bait.

These cases fit into a comprehensive picture. Hunger drove the rats to examine and nibble the baits and the harmlessness of the plain base as well as of Egyptian squill was discovered. But the same process of sampling applied to the toxic bait produced a renewal of shyness in the course of eating. In view of this method of approach we cannot be surprised to see that when Ranson tried to break down the shyness of his rats to toxic red squill by prebaiting, 13 out of 14 rats took the pre-bait readily but most of them refused the poison bait on the fourth day. There were only two complete takes and three sample takes, though we do not know if there were any signs of tentative sampling in the form of tooth marks on the rest of the baits. Similar behaviour occurred 110 days later with the same rats during their last squill bait. Sampling does not prevent all animals from consuming a poison bait, probably because of differences in memory and ability of association. In some, hunger drive was apparently stronger than shyness; also, varying susceptibility to poison might have contributed to making some animals less shy than others. This happened with other poisons besides red squill.

Sampling may not only lead to discrimination but also to reinforcing refusal even of plain bait. After a previous poison bait of low dosage a second identical one was only nibbled; this in turn strengthened refusal behaviour towards the plain base.

Another important conclusion emerges from the red squill experiment especially, that consumption of plain base within 24 hours does not mean the absence of shyness. General rise of alertness, slow feeding and sample take are probably responsible for the low consumption of poison bait by experienced rats, even after an attitude of strict shyness had been overcome.

8. Individual Variations in Behaviour

On several occasions individual rats did not behave like the majority. Some animals com-

pletely or partly refused even an initial bait—their number is small but not without significance. The reason for such initial refusal is not known; it might have been due to a "new object" reaction to food hitherto not encountered or a higher state of alertness than in the majority. As already mentioned, the general level of discrimination rose in successive treatments but again some individuals were above or below the average. In choice tests some refused new and known baits alike, some took only samples even of an entirely new poison in a new base. Besides an apparently greater caution and individual ability to discriminate, there were also proofs of an individual strength in the shyness acquired and in memory for baits. In the red squill test one rat remembered an initial poison bait for 52 weeks and constantly refused further squill baits, others took a subsequent poison bait after few weeks. In this test no two rats behaved completely alike, though only a few were outstanding individuals.

There were also some animals with little ability to discriminate; they accepted the same bait repeatedly. There also exists an individual susceptibility to poisons, as was clearly demonstrated for barium carbonate and red squill.

APPENDIX: SENSORY AND MENTAL CAPACITIES OF WHITE AND BROWN RATS.

The vast literature on the white rats behaviour has been summarised in reference books such as those by Munn, Maier & Schneirla, and Katz. Although very few of the experiments were made in task-free natural conditions requiring the use of all mental and sensory capacities, nevertheless some points of interest emerge which are relevant to our results. The possibilities of applying these observations to the complex behaviour of wild brown rats are mentioned and some field observations are added.

1. Sensory Faculties

Smell and Taste

From the review of available literature in the above reference books there is little and contradictory experimental work on the sense of smell in rats. And yet in any observation of rats, either white or brown, much sniffing and smelling may be noted.

The existence and varying acuity of olfaction was demonstrated in more recent experiments by Clyde E. Keeler (1942) on the association of the black gene with behaviour. Tests on the repulsive action of garlic were made on 125 F₂ crosses from three Albino Wistar

females with a gray Norway male. Most albinos required twice as much time (9.8 seconds) to back away from the garlic as the majority of pigmented, gray and black animals. In another test ten Hatai black-hooded rats backed away from garlic after an average of seven seconds whereas Wistar albinos never did the same, and some even began to taste the garlic. Keeler concluded that dullness of the olfactory discrimination is brought about by the albino gene. A case where olfactory discrimination prevented the intake of poison bait was mentioned in the main paper.

The sense of taste has been also insufficiently examined in previous papers (Munn: 150-151). Yet Doty (1945) was much impressed by the "very delicate sense of taste" of wild rats. He was able to quote a number of papers to support his opinion. According to his review rats were able to regulate their salt intake according to their needs in experiments on self selection (Richter & MacLean, 1939). Richter (1939) found that his rats detected salt in solutions of 1:2000 of water. The thresholds of recognition of salt by humans and rats agreed closely (Richter & MacLean, 1939). Rats were also able to distinguish between sucrose solutions and distilled water at 0.5 per cent while human beings could do so at 0.71 per cent solution (Richter & Cleasby, 1941). The same authors studied poison detection by rats in a taste threshold study with phenylthiocarbamide a bitter toxic substance. Very low concentrations of 0.0003 per cent in drinking water were detected and refused equally by rats and humans; but even lethal doses were accepted by rats when mixed with food.

Self selection experiments gave results which may go beyond discrimination by taste. Franke & Potter (1936; according to Doty) demonstrated the ability of rats to recognise diets of varying selenium contents. Katz (1937: 170) mentions investigations by Hausmann (1932) on the behaviour of albino rats in choosing foods and stimulants. The regulation and mutual balancing of the various components depended to a large degree on the ultimate usefulness for metabolism. In experiments by Harris and others and quoted by Katz (pp. 172-173), vitamin B depleted rats discriminated and selected a diet, which contained it, when they began to suffer from deficiency. In a large choice of food, experience enabled rats to make the correct choice in future.

In field conditions wild rats chose some food and left another similar kind untouched. In grocery stores for example we have found only special kinds of soap and fats attacked. Doty's account (1945: 158-161) of the discrimination of thallium poisoned oats by wild rats in his field tests is especially of interest, because the poison is described as tasteless and odourless and acts very slowly. After an initial experience the poisoned oats were increasingly avoided while plain oats were readily eaten. Doty had similar experiences with red squill baits, which were also subjected to "selective eating" after an experience. His remark that "the decision to eat the bait or to refuse it rests on the taste at the time of eating" reminds us of our own observations and conclusions that taste revives memory.

Finally we can assume that rats have considerable faculties of taste discrimination. It is therefore not surprising that a sample of arsenic with acid taste failed in the field, in spite of a high toxicity.

Vision

Evidence of colour vision is scarce and controversial (Maier & Schneirla, p. 292, Munn, p. 131). The histological structure of the rat eye makes a certain colour blindness understandable and it may be that this faculty "plays an unimportant part, if any, in the life of most mammals" (Maier & Schneirla, p. 300).

Not so brightness. "This type of discrimination is most elementary for the rat" (Munn, p. 124). The general conclusion from some observations on wild rats was that, although they may notice changes in lighting, their feeding behaviour was not strongly or permanently affected. Experimental evidence on the whole indicates some detailed vision and discrimination of shapes and patterns (Munn, p. 137). New objects, placed in their accustomed environment, caused a marked, sometime striking, reaction.

It may be that the discrimination between poisoned wheat and plain oats in one of our experiments was due to form discrimination. There are also some opinions and observations indicating that rats are myopic and perceive rather the movement of objects than the objects themselves. There is no doubt that their range of visual perception is inferior to that of humans.

There are again differences between white and pigmented rats. Lashley, according to Munn (p. 138) found hooded rats superior to albino rats in discriminating visual striations. Russell (Munn, p. 139) observed that pigmented rats were more accurate in judging the distance they were trained to jump and the force they used to perform the jump, and showed better consequent adaptation than albinos. In maze running white rats ascertained the closing or opening of a passage at distances of about 18 inches, pigmented rats at 30 inches. The pigmented animals remained superior at all stages of the experiment (Robinson & Weaver, acc. to Munn, p. 191-192).

Other Senses

Proprioception, tactual and kinesthetic senses have been investigated by many authors. Opinions vary widely as to the importance of kinesthesia in rats' movements; but most observers agree that rats have a fine touch and good spatial feeling. Blind white rats were able to discriminate fine differences of inclinations; a difference of 4° was discovered by 96 per cent, of 3° by 70 per cent, of 2° by 52 per cent, and 1° by 13 per cent of the participating rats. (Ruch, 1927, 1930 acc. to Munn, p. 153). Some evidence was found that the vibration rates of different parts of flat surfaces, used as runways, resonated differently when rats run over them (Shepard, 1929, acc. to Maier & Schneirla, p. 383). When such floors were removed many more errors in maze running and much hesitancy occurred (Curtis, 1931, acc. to Maier & Schneirla, p. 385). Using infra-red radiation in observations on wild rats in field conditions, Southern, Watson & Chitty (1946) found that rats became aware at a distance of newly placed objects in what, to the human eye, was complete darkness. The distance at which they stopped when approaching such subjects was usually shorter than under daylight conditions. It seems therefore that rats have good dark vision or, more probably, a well developed spatial sense. A certain sense of time in wild rats was perhaps demonstrated by their appearance at fixed times during token baiting in the field, undertaken in our control work. According to Munn (p. 307) experimental rats discriminated between delays of one to four minutes and in another case of ten seconds.

2. Complex Phenomena of Behaviour

Rodent control is often confronted with more complex kinds of behaviour than those usually analysed by animal psychologists. All sensory capacities work together in a wild animal's daily life, furthermore higher mental activities are involved and the powerful factors of "wildness" and fear add much to the complexity.

In discrimination, sample take, refusal and memory of poison bait probably various senses co-operate, associations and "attitudes" are formed. Rats obviously gain by an unpleasant experience; they learn. Hence the difficulties of rodent control. Katz (1937: 44-45) remarked on the superiority of the wild rat in "intelligence" over the white rat, "the experimental animal *par excellence* of the animal psychologist." A great mass of observations on isolated phenomena of behaviour has been accumulated by experimenters, but thoroughly analysed field observations are necessary to bridge the gap between these experiments, "which are more or less an artificial product" (Katz, p. 55-57), and behaviour in field conditions. We give here one example.

Live trapping experiments on wild and white rats (Thompson, 1953) illustrated the difference in the mentality of both. Wild rats in a field experiment entered an open trap, with the back door not closed, only after a lag of several days; their feeding inside the trap was continuously interrupted by flight reactions; the noise of negotiating the treadle dipping door disturbed and frightened many. When the trap was set, and the normal escape route through the back door closed, the rats caught reacted in a few minutes by showing increasing fear and restlessness. A marked trap shyness was observed in these observations.

The behaviour of white rats was entirely different. A similar trap set in a cage caught 10 out of 18 rats within 10 minutes. These were marked and released and after 10 minutes several of those marked were caught again. No trace of nervousness, nor of shyness and caution was visible.

Very interesting observations on learning and its influence on behaviour showed that out of many wild rats some few mastered the passage through the treadle in the "Wonder" trap. This knowledge gave them confidence in entering even a set trap; others caught at the same time did not profit from these exploits.

Some light on the difference between white and wild rats is thrown by experimental psychologists. Buytendijk & Fischel (1931) concluded that experience accumulates in rats and influences future behaviour. Munn (p. 244) produces positive evidence that "learning of one task influences the learning of further tasks." And later (p. 258) he says: "Not only previous maze practice but also the general adaptation to laboratory surroundings, handling, etc., brings about a favourable transfer" of learning.

3. Individual Behaviour

The case of the few rats which mastered the Wonder trap brings us to the broader issue of individual abilities. We saw that some white rats behaved in their approach to poison baits differently from the majority, and the term "individual behaviour" was used. In field observations, marked wild rats gave striking evidence of individuality in feeding, bait approach and shyness, and the hard core of residual populations, which are so difficult to exterminate, may be composed of such individuals.

Experimental evidence supports the conception of individual differentiation in sensory and mental abilities of rats. Munn (p. 276-8) quotes investigations by Tryon (1931) who found a "fairly consistent tendency for the rats, which manifested a certain performance in one maze to show a performance of similar rank in another. Individuals differ also in their 'capacity of association.'"

4. Fear, Wildness and Genetic Constitution

The approach to traps, described above, illustrates the importance of fear in a wild animal's life. Experimentally the effect of "emotional disturbance" in learning a maze was studied by Higginson (1930, acc. to Munn, p. 263). The results showed an increase in the time required for learning, in the degree of variability, the numbers of errors and the number of trials necessary for the mastery of tasks.

The fear factor thus described as important even in albino rats, increases with pigmentation. In experiments by Tryon (1931, acc. to Munn, p. 274) pigmented animals made poorer records than the albinos, because their greater sensitivity led them to be disturbed by slight movements of curtains and doors within the maze. Where there were no disturbances albino rats behaved more "stupidly" than pigmented ones according to Buytendijk and Fischel. Various opinions have been quoted before about the greater acuity of senses in pigmented animals. Munn (p. 275) drew the general conclusion that genetic constitution determines maze performance to a large extent. Differences in that constitution are expressed not only in pigmentation but also in reactions of wildness. In Keeler's tests hybrids bearing a grey coat were wilder than those having a black coat. Fear increases with wildness making such

animals unsuitable for maze experiments (Maier & Schneirla, p. 420) but giving wild animals a powerful equipment for their ordinary task in their normal environment.

5. General Conclusion.

Many of our experimental results with white rats would be applied successfully to field conditions dealing with wild rats. There were, however some difficulties, as the behaviour of wild rats is more complex and difficult to reduce to simple principles. The basic mental equipment of both white and wild rats is probably the same, but their acuity of senses, range of experiences and state of alertness differ greatly because of wildness and fear.

SUMMARY

Experiments on the acceptance of successive poison baits made with white and few brown rats, showed marked change of behaviour after survival after initial baits. It was found that the food medium, the base, was mainly responsible for a subsequent reluctance or refusal to eat. Rules of this behaviour were established and the term "base shyness" substantiated. Base shyness may develop within a wide range of time from half an hour to several days depending upon the effect of a particular poison, degree of illness, nature of base. Successive experiences may reinforce or overwhelm previous ones. Memory of poison bait may last in the case of red squill for more than a year in individuals, for other poisons at least for two months. There were great individual variations in memory and ability of association. Unpleasant experiences cause a rise in alertness and may lead to discrimination of baits. This can be effected by sampling of baits in which taste memory is revived. A certain number of rats showed individual abilities above or below the average standard. In an Appendix a review of the literature and some field experiences are given; they show that the wild rat, additionally stimulated by fear and wildness, is superior to the laboratory white rat in acuity of senses and caution.

REFERENCES

- Buytendijk, F. J. J., & Fischel, W. (1931). Strukturgesamtes Verhalten von Ratten. *Arch. Néerl. Physiol.* 16, 55-83.
- Chitty, D., & Shorten, M. (1946). Techniques for the study of the Norway rat (*Rattus norvegicus*). *J. Mammal.* 27, 63-8.
- Dopmeyer, A. L. (1936). Plague eradication measures on the island of Maui, Territory of Hawaii. *Publ. Hlth. Rep., Wash.* 51, 1533-56.
- Doty, R. E. (1938). The prebaited feeding-station method of rat control. *Hawaii. Plant. Rec.* 42, 39-76.
- Doty, R. E. (1945). Rat control on Hawaiian sugar cane plantations. *Hawaii. Plant. Rec.* 49, 71-239.
- Hamilton, W. J., Jr. (1936). Rats and their control. *Bull. N.Y. St. agric. exp. Sta., Cornell*, No. 353: 1-32.
- Hatcher, R. A., & Weiss, S. (1923). Studies on vomiting. *J. Pharmacol.* 22, 139-93.
- Jaffé, R. (1931). Anatomie und Pathologie der Spontanerkrankungen der kleinen Laboratoriumstiere . . . Berlin.
- Katz, D. (1937). Animals and Men. Studies in comparative psychology. London.
- Keeler, C. E. (1942). The association of the black (non-agouti) gene with behaviour in the Norway rat. *J. Hered.* 33, 371-84.
- McDougall, W. A. (1944). An investigation of the rat pest problem in Queensland canefields: 3. Laboratory experiments on food intake and toxicity. *Queensland J. agric. Sci.*, 1, No. 3: 1-32.
- Maier, N. R. F. & Schneirla, T. C. (1935). Principles of animal psychology. pp. 1-529. New York.
- Munn, N. L. (1933). An introduction to animal psychology: the behaviour of the rat. pp. 1-439. Cambridge Mass.
- O'Connor, M. G., Buck, R. E. & Fellers, C. R. (1935). Red squill investigations: properties, toxicity, and palatability of red squill and powder baits to rats. *Industr. Eng. Chem.*, 27, 1377-80.
- Pemberton, C. E. (1925). The field rat in Hawaii and its control. *Bull. Hawaii. Sug. Ass. Ent. Ser.* No. 17, 1-46.
- Schwartz, E. W. (1920). Toxicity of barium carbonate to rats. *Bull. U.S. Dep. Agric.* No. 915: 1-11.
- Southern, H. N., Watson, J. S. & Chitty, D. (1946). Watching nocturnal animals by infra-red radiation. *J. Anim. Ecol.* 15, 198-202.
- Thompson, H. V. (1953). Experimental live trapping of rats, with observations on their behaviour. *Brit. J. anim. Behav.*, 1, (3), 96-111.

Note on the Behaviour of Desert Locusts in a Light-Beam

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Night-flying Desert Locusts (*Schistocerca gregaria* Forsk.) have been observed coming to light on a number of occasions (see e.g. Kennedy 1939), but little information as to the nature of the reactions concerned has so far been recorded. The present note reports some observations of such behaviour, on the Red Sea coast of Saudi Arabia, which provide some evidence on the mechanism of the reactions involved.

The observations were made 100 miles south-east of Jedda, near Mujairima, on 15 February, 1950, on the edge of a large *sabakha* (salt-flat) bordered by low sand-dunes with *Suaeda* bushes. No locusts were seen on arrival in the area in the late afternoon; the first one was noticed at about 19.25, some 65 minutes after sunset, at the light of a single 6-watt inspection lamp. At 19.30 the headlights of a Landrover were switched on, giving a divergent, mainly horizontal beam; each lamp consists of a 36-watt bulb fitted in a parabolic reflector with a vertically fluted lens, giving a light distribution equivalent to a 21,000 candle-power source along the axis of the lamp and to a 1,000 candle-power source when viewed from some 6° above or below or from 11° to the side of this axis. Fifteen locusts—5 males and 10 females—were collected in ten minutes, and a number of others escaped.

The specimens approached phase *solitaria* both in general appearance and biometrically. The ratio of femur-length to head-width (F/C) gave mean values and standard errors of $3.78 \pm .05$ for males and $3.79 \pm .036$ for females, which agree closely with the mean values quoted by Dirsh (1951) as characteristic of *solitaria*. The ratio of elytron-length to femur-length (E/F) gave values of $2.06 \pm .02$ for males and $2.06 \pm .014$ for females, which may be compared with the figure of 2.055 used by Rao (1937) to separate phases *solitaria* and *transiens*.

During this season in the Mujairima area, as elsewhere on the Tihamah (coastal plain), adult *solitaria* had first been recorded in numbers following heavy rains in November 1949, and breeding of phase *solitaria* had subsequently been observed in this area (Ashall, 1950).

Weather conditions, recorded at 20.00, were cloudless sky, no moon; air temperature, by sling psychrometer, 73°F; wind northerly, about 5 m.p.h., after having been south-westerly by day. By 22.00 activity had much diminished, but occasional flying locusts were still seen, at heights up to 5 feet or so, at an air temperature of 69°. These temperatures are somewhat lower than those at which sustained night flight by phase *gregaria* has been reported. In Morocco in July 1927, Desert Locust swarms were recorded as migrating at night only at air temperatures above 80° (Regnier, 1931), and, during similar observations in central Asia two years later, night flight was said to become weak below 79°, with settling when temperatures fell below 75° (Predtechenskii, 1935).

Between 22.00 and 23.00, in an attempt to see whether locusts were still present in numbers in the immediate vicinity, the Landrover was driven for about a mile through the dunes near the camp. Only four settled locusts were seen, though they showed up conspicuously on the *Suaeda* in the headlights, and only one locust was seen in flight. At about 08.00 the following morning, in bright sunshine at an air temperature of 72°, only two locusts were flushed in the course of a further mile by Landrover through the same area of *Suaeda* dunes.

The number of locusts seen at light was surprisingly large—up to half a dozen or so at a time—particularly in relation to the low density of the population seen in the vicinity both later the same night and the following morning; and the locusts were flying strongly, particularly during the earlier part of the evening, when numbers of them disappeared from sight still 10 feet or so up. Rao (1937) first demonstrated that the migration of Desert Locusts occurs in the solitary as well as in the gregarious phase; and our impression on this occasion was in fact of sustained flight by a moving population, rather than of casual short flights by a stationary local one.

Flight within the illuminated area was characterised by repeated turns, in vertical planes as well as in the horizontal one, and noted as

being most acute in the most strongly illuminated area; in fact in the direct beam of the headlights, up to say 20 yards ahead and say 5 feet in height, stable horizontal flight was not observed at all. Locusts which had temporarily settled within this area were repeatedly seen executing a characteristic "stalled turn" manoeuvre—climbing very steeply after the initial jump into the air, then making a sharp turn in a vertical plane (several times giving the impression of presenting the ventral surface to the direction of the light), and finally diving heavily into the ground. None of the locusts observed in this condition showed any signs of beginning to recover the power of normal flight so long as they remained within the brightly illuminated area, though the actual intensity of illumination which they were experiencing was much less than that of sunlight. Partly mature Desert Locusts of phase *gregaria* have since been observed (by C.A.) behaving in a similar way at light, in north-central Arabia, some 63 miles north of Marrat, on 3 May, 1951.

None of the locusts were ever seen to fly steadily towards the light, so that the behaviour observed cannot be described as photo-tactic (Fraenkel & Gunn, 1940). There was in fact no evidence of any actual attraction of the locusts to the light; and the relatively large numbers seen at a time appeared to represent a trapping effect resulting from the loss of stability in flight (*vide infra*) experienced by locusts entering the illuminated area. A similar effect may perhaps have been involved in the moth behaviour recorded by Robinson (1952), with "an annular area many yards from the lamp in which insects entering the area at low velocity seem undecided and flutter about for some considerable time before flying away." Photo-taxis might perhaps be envisaged as having operated beyond the range at which we were able to see the locusts flying in the beam, and hence to have contributed to the numbers seen, though locusts were repeatedly seen entering the beam from the sides, and none were actually seen making their way up the beam. Robinson and Robinson (1950) consider it improbable that the assembly of moths at a light source is due to actual attraction, and Robinson (1952) quotes marked effects, upon the catch, of small changes in the position of a light-trap, as evidence that the principle involved is not one of attraction. Detailed records of the distribution of egg-laying by the Red

Bollworm moth, *Diparopsis castanea* Hmps., on cotton crops in the vicinity of acetylene light-traps in the Transvaal have similarly demonstrated the very restricted area affected by each of the latter (Parsons, 1932).

The behaviour seen might perhaps be interpreted as klinokinesis (Fraenkel & Gunn, l.c.), in which the frequency or amount of turning per unit time depends on the intensity of stimulation; it was particularly noted that the changes of course exhibited by the higher-flying locusts, which only just became visible in the top of the beam, were much less violent than those shown by the more brightly illuminated individuals nearer the axis of the beam and closer to the lights. A difficulty in interpreting the reaction as a simple klinokinesis is the fact that the turns seen were characteristically executed in the vertical as well as in the horizontal plane, in a manner which we have not observed in locusts flying by day, and furthermore appeared to involve loss of stability in flight. This latter impression was accentuated by unusually clumsy landings, exemplified by the single flying locust recorded during the night traverse of the *Suaeda* dunes, which, entering the beam of the headlights of the temporarily stationary vehicle from the side, struck the rising surface of the dune ahead with such violence as to bury the head and part of the thorax in the sand.

The behaviour seen appears to have something in common with the dorsal light reaction exhibited by a number of free-swimming animals, in which the normal orientation is maintained by presenting the dorsal surface to the direction of the light, normally coming from above (Fraenkel & Gunn l.c.). The effects recorded might in fact be consistent with a confusion of the predominantly horizontal direction of the beam with the vertical. Such a confusion might be expected to cause changes of orientation about a transverse (pitching) axis when the initial orientation is towards (or away from) the light, and about a longitudinal (rolling) axis when the initial orientation is across the beam. Changes of orientation about a pitching axis result in climbing or diving, at angles which might be expected to approach the vertical if the confusing stimulus were sufficiently strong, while changes of orientation about a rolling (banking) axis would lead to turning if, as seems likely, the flying locust has more side area behind its centre of gravity than

ahead of it. The "stalled turn" seen could be interpreted as incorporating all three of these effects in their most marked form—a near-vertical climb, a very sharp turn and a near-vertical dive.

The effects recorded would in fact be completely consistent with a dorsal light reaction, but for the evidence, such as it is, that the locusts presented the ventral instead of the dorsal surface to the light. It was by no means easy to follow the orientation of the locusts during these evolutions, since attention was usually drawn to a particular individual concerned only by its actual take-off. All that can be said is that an impression was gained that the ventral surface was presented to the light during the actual turn, and additional observations on this point are particularly to be desired. We cannot be certain that it did in fact occur during all the stalled turns observed, nor can we say whether the ventral surface was presented to the light during the climb and dive as well as during the turn itself.

Fraenkel & Gunn (l.c.) have suggested that flying insects may be inherently stable owing to the dorso-lateral position of the wing articulation, above the level of the centre of gravity. The present observations however indicate that there may also be an important visual element in the maintenance of the normal orientation of the flying locust, which further observations might help to elucidate.

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REFERENCES

- Ashall, C. (1950). Report of the Saudi Arabia team, Desert Locust Survey, for 1949-50 (unpublished typescript).
- Dirsh, V. M. (1951). A new biometrical phase character in locusts. *Nature*, London 167, 281.
- Fraenkel, G. & Gunn, D. L. (1940). The orientation of animals, Oxford 352 pp., 135 figs.
- Kennedy, J. S. (1939). The behaviour of the Desert Locust in an outbreak centre. *Trans. R. ent. Soc. Lond.* 89, 385-542.
- Parsons, F. S. (1932). Summary of work on cotton insect pest control at Barberton, Transvaal. *Reports from Experiment Stations* 1930-31, 16-17. Empire Cotton Growing Corporation, London.
- Predtechenskii, S. A. (1935). Studies on the Desert Locust in Central Asia and Transcaucasus in 1929-30. *Bull. Pl. Prot. Leningr.* 11, 1-92.
- Ramchandra Rao, Y. (1937). A study of migration among the solitaires of the Desert Locust. *Proc. 4th. Int. Locust Conf.*, Cairo, app. 10: 14 pp.
- Régnier, P. R. (1931). Les invasions d'acridiens au Maroc de 1927 à 1931. *Dir. gén. Agric. Colonis. Déf. des Cult.*, Rabat 3, 139 pp.
- Robinson, H. S. & Robinson, P. J. M. (1950). Some notes on the observed behaviour of Lepidoptera in flight in the vicinity of light sources. *Entomologists' Gazette*, London, 1, 3-20.
- Robinson, H. S. (1952). On the behaviour of night, flying insects in the neighbourhood of a bright source of light. *Proc. R. ent. Soc. Lond. (A)* 27, 13-21.

The Grazing Behaviour of Dairy Cattle at the National Institute for Research in Dairying

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Introduction

Methods of increasing the production from grassland by using special purpose leys, increased quantities of fertiliser and systems of controlled grazing are now widely known and appreciated. Unfortunately, we have little or no detailed information as to the best way of utilising this increased production to make the fullest use of the sward nutrients, especially by dairy cattle. Improvements in grazing technique are of primary importance in this direction, and with this requirement in view the present study was commenced, first, to obtain a fairly detailed picture of the normal behaviour of dairy cattle, particularly when grazing and secondly, to use this information in order to make suggestions for improving methods of grazing management.

Two series of observations were undertaken. (1) The detailed observation of the behaviour of four cows for periods of 24 hours, on four occasions, and (2) the observation of the behaviour of a dairy herd for periods of 24 hours at monthly intervals for twelve consecutive months.

These will be dealt with separately.

(1) Observations on Four Cows

Our object in these observations was to secure a complete behaviour pattern over the 24 hr. period and to record the length of time which individual cows spent grazing, lying down, loafing and ruminating. Records of the number of times the animals drank, defaecated and urinated and the distance walked were also kept. The following definitions of the behaviour were made:

Grazing time covered the entire period in which the cow spent searching for and eating herbage.

Lying-down time was the total time the animal was reclining whether ruminating or not.

Loafing time was the remainder of the time,

i.e. the time spent walking and standing up but doing nothing specific except some chewing of the cud.

Ruminating time was the entire period covered by the acts of regurgitation, the chewing of the bolus, and deglutition, including intervals between boluses.

Four 24 hr. observations, each commencing at 8.0 a.m., were completed. On each occasion four Dairy Shorthorns in milk were confined in a temporarily constructed one-acre paddock containing a large tree for shade and a water trough. Observers, working on a shift system, observed the cattle continuously, milking times included. The four observations were completed in a period of eight weeks, three while the animals were on an old ley and one when grazing a maiden ley. Weather conditions were similar during the four watches apart from minor differences in temperature and a little rain on two occasions.

Results

The results of the four observations are summarised in Table I.

Table I

Observation No.	1	2	3	4	Mean
<i>Hours</i>					
Grazing	7.96	5.87	7.31	4.94	6.52
Lying down	7.72	9.18	8.92	11.07	9.22
Loafing	8.33	8.95	7.77	7.99	8.26
Ruminating	4.68	6.34	4.92	6.47	5.60
<i>Number of</i>					
Defaecations	10	13	12	11	11.5
Urinations	10	11	11	7	9.8
Drinks	4.00	2.75	4.75	3.50	3.8
Distance walked yds.	3,960	1,950	3,240	3,090	3,060

At this stage we do not wish to draw any definite conclusions from such limited observations, but merely to state our results as recorded.

Grazing. The average time spent in grazing during the observations was 6.52 hours with an individual range from 4.33 to 10.48 hours. It will be observed that during observation number 1 when the cows were on an old ley with a short growth of grass, they grazed for a longer period than in observation number 2 when on the maiden ley with 6-8" of leafy growth. When the cows were returned to the original old ley (observation number 3) the average grazing time increased. However, during observation number 4 when the cows were on another old pasture, grazing time was reduced. This latter grazing was of a very poor type and, as it was now late in the season, may not have been as palatable to the cattle as previously.

The proportion of the total time spent grazing between the two milkings, did not vary very much either between cows or pastures. About equal lengths of time were spent grazing in each of the two periods.

The length and distribution of the individual grazing periods will not be discussed at this stage as the point will be observed more clearly in the results from the herd watches.

The milk yield of each cow credited to the plot under observation did not appear to be in any way related to the length of time spent grazing. The number of separate observations was small and the correlation obtained was non-significant. This was to be expected under our conditions, for apart from the other factors which control milk yield, there was no evidence that the total time spent grazing (as defined by us) was in any way related to the quantity and quality of dry matter consumed. It should be noted that the animals were all receiving concentrates which would undoubtedly affect the time spent grazing.

Lying down. The average time spent lying down during the four observations was 9.22 hours; the longest time devoted to one specific action. The individual times were not related to the current daily milk yield of the animals. A correlation of -0.942 was found between the mean times spent lying down and the mean grazing time, and it would seem that the longer time a cow grazes the less time she spends lying down. It is noteworthy that only 14.5% of the total time spent lying down was between the a.m. and p.m. milkings.

Loafing. The time which the cows spent in the cowshed is included under the definition of loafing, but even when this period of $3\frac{1}{2}$ hours is accounted for there is still a difference of over 4 hours to be explained in the field. This length of time proved to be very constant and may have some unexplained significance.

Ruminating. Ruminating time occupied 5.60 hours each day of which 4.52 hours (or 81%) occurred when the cows were lying down. This preference for ruminating whilst lying down was very marked except during wet periods when the animals ruminated whilst loafing.

Defaecations and Urinations. The average number of defaecations and urinations in each 24 hr. period was 11.6 and 9.8 respectively. The distribution of the dung and urine during the 24 hours is of interest and details are given in Table II. From this Table there is possible evidence of a transference of fertility from day to night pastures.

Table II

Period	Excretions: Percentage of total number	
	Defaecations	Urinations
Day Pasture	36	35
Night Pasture	52	59
Cowshed and Road	12	6

Drinks. The average number of drinks in 24 hours was 3.8. The number of drinks was higher (average 4.1) when the cattle grazed the old ley and was reduced to 2.75 when on the maiden ley. Our data also suggest that apart from a drink on reaching the field after the afternoon milking, water is not required during the night interval. A fact which may be of great importance in the utilisation of land which lacks adequate watering facilities.

Distance Walked. The total distance walked by the cows under observation in the paddock averaged 3,060 yds. (1.74 mile). It can be seen from Table I that when the animal was on the old ley with little keep available she walked 3,000 yards per day, once almost 4,000 yards, whereas when she was grazing the maiden ley with abundant herbage the distance covered was less than 2,000 yards. This would suggest that on barer pastures the cattle have to travel further in searching for sufficient herbage to satisfy their nutritive requirements and would

justify the increased allowance of S.E. recommended by conventional feeding standards when animals are grazing on a poorer pasture. A shorter distance was walked in the night interval than in the day although grazing times were about equal which tends to support the observation that at night, grazing was of a more determined character than that during the day.

(2) Herd Observations

In an endeavour to build up a picture of the behaviour pattern of an entire dairy herd under normal conditions of management a series of twelve observations was made at monthly intervals for a complete year. The herd observed was the one owned by the Institute and consisted of Shorthorns with a few Guernseys. The average number of cattle in the herd was

fifty-two. As in the previous observations the cow's day was divided into the time spent grazing (or eating), lying down and loafing, but it was found impossible to record other activities apart from ruminations on a few occasions. The observations commenced at 8.00 a.m. and lasted for 24 hours excluding milking times, and records were kept of the number of animals engaged in each activity every five minutes when it was light and every 15 minutes during the hours of darkness.

The twelve observations can be conveniently divided into two parts (a) observations under conditions of "winter" management, and (b) observations under conditions of "summer" management. The winter results are not strictly concerned with the grazing of herbage but serve as a useful introduction to, and confirmation of,

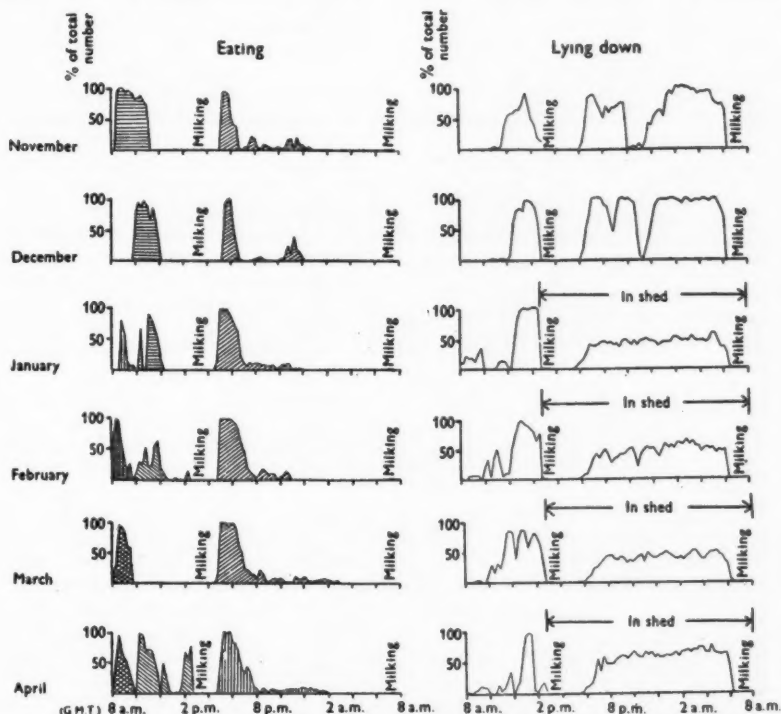


Fig. 1. The behaviour of the herd of dairy cows during the Winter months.

Key to Foods eaten:

Diagonal hatching Left to right = Grass
Right to left = Hay and Roots
Horizontal hatching = Kale

Vertical hatching = Hay
Square hatching = Silage
Diamond hatching = Hay and Silage

the data obtained when the cattle were on an all-grass diet.

(a) *Winter Management.* These results are illustrated graphically in Fig. 1. Only details of eating and lying down are given, and for ease of interpretation, the number of cows has been expressed as a percentage of the total during each particular observation. The feeding and management of the herd varied considerably during the six-month winter period but certain definite trends are evident from the data. For both the eating and lying down curves, there is a great deal of similarity even when conditions of feeding and management are different. When conditions are practically identical, e.g. in November and December, the graphs are

almost identical and reflect a definite behaviour pattern under a given set of environmental conditions. Throughout, the time of milking affects the behaviour pattern but it is evident that there is a major peak of feeding immediately the animals enter a field after milking or when a new food is offered (e.g. in January and February). When out at grass in November and December, the herd was very restless about midnight and ate any portions of the kale left from the earlier feed. When in the cowshed there was no such marked secondary peak of feeding, although the animals picked at their food residues for a longer period in the evening.

The pattern of lying down was very similar when managerial conditions were similar. When

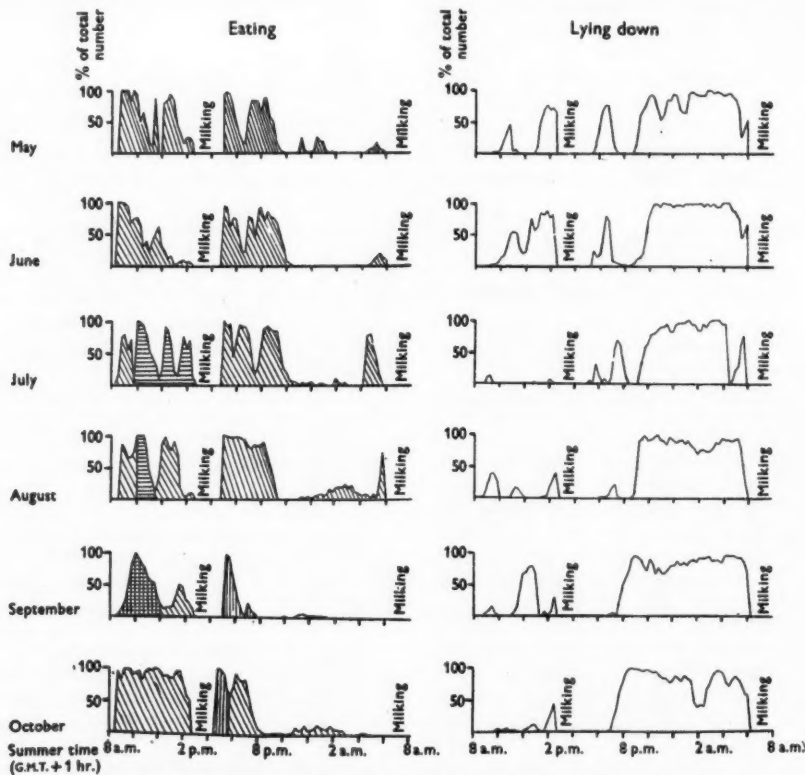


Fig. 2. The behaviour of the herd of dairy cows during the Summer months.

Key to Foods Eaten—Diagonal hatching = Grass
Vertical hatching = Hay

Horizontal hatching = Lucerne
Square hatching = Silage

the herd was out at grass day and night as in November and December, there were three main periods of lying down, (1) before the p.m. milking, (2) between the evening feed and midnight and (3) between the active period around midnight and 6.0 a.m. A few animals always preferred to stand up but the majority of the herd laid down in a sheltered position. The pattern of lying down during the morning was always of a similar type but during the night when the cattle were housed, this changed. When fastened up in the cowshed the animals were very restless, and at any one time only about 50% of the animals would be resting. There was constant movement and activity at night, and the failure of the cows to rest would suggest that under our conditions the cows would have been more comfortable if out of doors or in a straw yard.

(b) *Summer Management.* These results are presented graphically in Fig. 2 by the same method as the winter results.

In general a similar pattern of behaviour was observed throughout all the summer months. This was characterized by a grazing or eating peak immediately after the cattle entered the field, followed by a gradual decline in the numbers grazing until the afternoon milking, and a similar double or single grazing peak after the p.m. milking which steadily lessened until 10.0 p.m. There was very little grazing after this time except for minor bouts shortly before the cows left the field for the a.m. milking in July and August. On these two occasions the early period of light appeared to stimulate grazing activity which had to be interrupted because of the a.m. milking. When it was dark until 6.0 a.m. the cows made no attempt to graze and were all lying down when disturbed for the early a.m. milking.

It was also observed that there was a strong relationship between the time of sunset and the time when the majority of the herd stopped grazing and lay down. Approximately 50 minutes after sunset only 10% of the herd would be grazing, and 40 minutes later 90% of the herd would be lying down. With this evidence of the cows' general inclination to rest during the hours of darkness, it would seem necessary to make

some special provision for grazing cattle when it is dark for the entire period between the evening and morning milkings. This might take the form of special lighting arrangements in the fields, or even a drastic alteration in the hours of milking to allow grazing to proceed in the period of light.

A further point of practical importance arising out of both series of observations was the fact that the natural inclination of the cow was to divide her total daily grazing time about equally between the day and night intervals. Thus, if a herd is turned on bare pasture at night, a very common occurrence in practice, there is a risk that the animals' intake of herbage nutrients may be severely restricted. To avoid this it would appear advisable to have the day and night paddocks of about equal size and with herbage of a similar nutritive value.

The exact effect of these aspects of the grazing management of the dairy herd upon milk production have yet to be proved experimentally, but we consider that by studies of animal behaviour as outlined in our paper, we are a little nearer to answering a few of the problems concerning the pasture-animal complex.

Summary

- (1) The behaviour of dairy cattle under normal conditions of management is reported.
- (2) Under our conditions the cows grazed 6.52 hr., lay down 9.22 hr., loafed 8.26 hr., ruminated 5.60 hr., defaecated 11.6 times, urinated 9.8 times, and drank 3.8 times in 24 hours.
- (3) A very similar periodicity of behaviour during 24 hr. was observed throughout the year, especially when environmental conditions were similar.
- (4) The effect of light on grazing behaviour has been recorded.
- (5) Tentative suggestions for improving grazing management as a result of the observations are made.

Acknowledgments

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Hormones and the Maturation of the Central Nervous System with Special Reference to the Rat

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Many of the responses of an organism to changes taking place within its perceptual field are effected through the close integration of nervous and endocrine activity. This integration, whose nature has been discussed in general terms by Beach (1948) and with particular reference to the rat by Munn (1950), may be of three kinds. In the first place, the secretion or release of hormones may be stimulated by the nervous system either directly through the medium of secretomotor nerves (as for example in the release of adrenaline by the adrenal medulla), or more indirectly through the close functional association which exists between the hypothalamus and the adenohypophysis. Although the second of these mechanisms is almost certainly implicated in such phenomena as ovulation following coitus in the rabbit (Hammond & Marshall 1925), the oestrus response of the ferret to increased illumination (Thomson & Zuckerman 1953) and the changes in the reproductive organs (Fiske 1941) and the powers of lactation (Eayrs 1951 b) of the rat which are associated with alterations in the environment, the way in which the hypothalamus controls the pituitary is still imperfectly understood (see Zuckerman, 1953). Secondly, there is ample evidence that the nervous system in its turn responds to changes in endocrine activity. Changes occur in the excitability of nervous tissues after the administration of sex hormones (Herren & Haterius, 1931; Chauchard 1943), and rhythmic fluctuations in the amount of running activity in the female rat coincide with the different phases of the ovarian cycle (Wang, 1923). In man too, psychological outlook changes both as a result of fluctuations in ovarian activity during the menstrual cycle (Benedek & Rubenstein 1939) and of therapeutic administration of hormones (see Cleghorn 1952, Browne 1952). The third form of inter-relationship is that in which both the first two may be combined to provide essential links in a complex behavioural sequence. An example of such interaction is to be found in the seasonal migratory activity of birds (Rowan, 1931). As far as the

process is understood, changes in central nervous activity induced by the lengthening or shortening of the hours of daylight are communicated to the endocrine system and result in changes in the rate of secretion of gonadal hormone. These in turn modify the central nervous system in such a way as to alter the significance of the perceptual field and to lower its threshold for mediating the innately organised patterns of behaviour involved in migration.

These examples, which illustrate both the completeness and complexity of the integration of the nervous and endocrine systems have been taken at random from the behaviour of the adult individual. Immature individuals do not, on the whole, respond to their environments in the same way as do adults and the reasons for this must be sought in terms of differences in central nervous organisation, of endocrine secretion, or of both. The fact that both nervous and endocrine systems develop side by side in an orderly manner suggests that their ultimate close relationship may be laid down during ontogeny, but surprisingly little is known about their mutual interaction during this period. When, and how, these two systems come to influence each other so closely are questions to which a complete answer has yet to be found.

The substance of this communication deals with but one aspect of this problem, namely the influence of hormones on the maturing central nervous system. There are two ways in which this influence can come into play. In the first place, a hormone may act on an already differentiated nervous mechanism which is genetically determined and which develops independently of the endocrine organs ultimately destined to activate it. Secondly, in addition to regulating the metabolism of nervous tissues, endocrine secretions may exert a specific influence on the complicated processes involved in the differentiation of neurones and on the way in which they establish their functional inter-relationship. In the discussion which

follows both these propositions are examined in relation to the influence, during the early life of the rat, of two classes of hormone: the sex steroids and the secretion of the thyroid gland.

The Sex Hormones

The possibility that the sex hormones play a part in regulating the maturation and function of the central nervous system of the rat may be inferred from the sex differences in reproductive behaviour which ultimately appear in the adult. The many experiments which have been performed to elucidate the nature of this neuro-endocrine interaction make it clear that these sex differences are due to a direct and specific influence of the male and female sex hormones upon the central nervous system and that this influence is concerned, not only with the assembly of those elements of neuro-muscular activity, which combine to form the total pattern of sexual behaviour, but also with a re-orientation of the perceptual mechanisms responsible for the release of such behaviour (see Eayrs, 1952). It is accordingly of particular importance to know how far the behaviour characteristic of male and female is based on sex-specific patterns of central nervous organisation, and what part is played by the sex hormones during ontogeny in establishing this behaviour.

The answer to these questions is by no means clear-cut, but the trend of the experimental evidence does suggest a possible, if incomplete, solution to the problem. In the first place, it would seem that the neural organisation underlying sexual behaviour is laid down independently of the influence of the sex hormones. Beach (1945), for example, reports that a female rat in which all gonadal tissue was congenitally absent displayed normal mating behaviour with a male when injected with oestrogen. Furthermore it has been shown that when given androgen later in life male rats castrated at birth will copulate with receptive females (Beach & Holz 1946). An analysis of the effects of early castration and the subsequent treatment of genetic male and female with homologous and heterologous sex hormones shows that "neuro-muscular mechanisms capable of mediating the mating behaviour of either sex are present in both male and female" (Beach 1948). At the same time however the nervous system of the male shows a special affinity for stimulation by androgen while that of the female is more susceptible to the influence of female

sex hormone, facts which suggest that gonadal secretion may play a part in establishing a preferential relationship between one of these neural mechanisms and the genotypical sex hormone. This possibility is well illustrated by the development of sex-specific patterns of micturition in the dog. Such behaviour matures under the influence of the sex hormones and once established resists attempts to reverse it. Thus leg-lifting during the act of micturition cannot be evoked by giving androgen to mature bitches. On the other hand, administration of male hormone to newborn bitches, in which definitive sex-specific behaviour has not yet appeared, does result in the appearance of the characteristic male pattern (Martins & Valle, 1948).

Complex patterns of innate behaviour are built up of simpler components which, in the case of behaviour which normally appears after puberty, have a threshold for hormone facilitation lower than that for the complete response (Beach, 1944a; Berg, 1944). It might therefore be expected that the maturation of simple automatic behaviour whose first appearance in the rat follows a stereotyped and well-documented sequence (Small, 1899; Tilney, 1933; Anderson & Patrick, 1934), would also be subject to the influence of the sex hormones. This proposition has been tested experimentally by applying quantitative methods to the study of behaviour maturing during the first 24 days of life (Eayrs, 1951a). The results failed to reveal any sex differences in behaviour which appears during the first 15 days of life but such differences did appear in the only two responses studied which matured after that age. The first of these, the righting reflex, was tested by dropping the rat, back downwards, from a height of 10 inches and recording its ability to land on its feet. The presence or absence of the second, the placing reaction, was assessed by touching the animal's chin on a horizontal bar and observing whether it immediately placed both forepaws on the bar. Both responses matured earlier in the male than in the female. These observations suggest that, at about 15 days old, androgen may begin to facilitate central nervous maturation, and the fact that treatment with equine gonadotrophin, a hormone known to stimulate the secretion of an androgenic substance by the ovary (Bradbury & Gensbauer, 1939; Pfeiffer & Hooker, 1942), will advance the time of

appearance of the placing reaction in the female is consistent with this view.

The work of Hanson (1949) provides additional evidence that maturation does not proceed identically in the male and female rat. Groups of male and female littermates of various ages, beginning at 30 days old, were tested on the three-table apparatus described by Maier (1932). The results, which may be regarded as measuring functional capacity at the cortical level, showed that from the earliest age studied the male performed consistently better than the female.

These observations, while they provide no direct evidence concerning the mode of interaction between the sex hormones and the nervous system during maturation, do at least demonstrate a sex difference which might help to account for the affinity of the hormone of either sex for the nervous system of the genotype. The possible significance of a facilitatory effect on the part of androgen in this respect will be considered later.

The Thyroid Hormone

The diseases associated with thyroid deficiency in man have been known for many years. A characteristic difference between the two principal manifestations of the disorder, congenital hypothyroidism (cretinism) and myxoedema, is that the mental functions of the cretin usually fail to respond to replacement therapy whereas in myxoedema recovery is frequently complete (Means, 1948). This strongly suggests that, in addition to its functions in the control of tissue metabolism, the thyroid gland plays a prominent part in regulating the maturation of nervous tissues. Such a hypothesis, as far as the rat is concerned, can readily be tested experimentally. One of the ways in which this can be done is by giving methyl thiouracil, a drug which prevents the synthesis of thyroid hormone by the gland.

Rats made cretinous in this manner appear rotund by reason of a brachicephalic skull, a distended abdomen and erected infantile hair. They are cold to the touch, have a basal metabolism which is about 60% of that of normal rats, and although their growth, as measured by body weight, is not appreciably retarded during the first 15 days of life their bodily proportions are already deviating from the normal. At 24 days old they are considerably smaller than normal littermates.

These physical characteristics are associated with marked changes in behaviour. The cretinous

rat is sluggish and does not usually play with its littermates; yet when stimulated it is capable of astonishing, and at times almost convulsive, activity. The maturation of automatic behaviour in the experimental cretin follows the same general plan as in the normal animal, but is grossly retarded as the following previously unpublished observations show:

(a) Reflex Suspension

If, after the age of 5-6 days, the rat's forepaws be touched against a horizontal wire it will usually grasp the wire and cling for a limited time. The duration of clinging in the normal rat increases with age and at the same time the pattern of the response, which is initially one of passive suspension, changes by about the 12th day to one of co-ordinated limb movements which resemble those used in climbing. This change is believed to mark the assumption of cortical control over neuro-muscular activity (McGraw, 1943). In the cretin the duration of clinging does not increase to the same extent as does that of the normal, and the pattern of behaviour at 15 days old is still one of passive suspension.

(b) After-discharge

If the tail of an infant rat be pinched, the animal is thrown into periodic convulsions which take up to one minute to die out completely. This convulsive response disappears as the rat grows older and the sequence of changes in behaviour which ensue (see Tilney, 1933) is attributable to the maturation of cerebral inhibitory centres. Convulsions last longer in the cretin than in the normal rat, and their ultimate elimination from the rat's behaviour occurs at a later age.

(c) Righting Reflex and Placing Reaction

Both these patterns of behaviour, already referred to in relation to the influence of the sex hormones, mature significantly later in the cretin than in the normal rat.

All these observations suggest that the retarded behavioural development of the cretin is due to an impairment to the maturation or function of cerebral co-ordinating centres. Although these centres are not generally well defined anatomically, the placing reaction is known to depend on the integrity of a clearly localised region of the frontal lobes of the cerebral cortex (Brooks, 1933). This part of the brain has therefore been examined for structural changes which might be correlated

with the differences in behaviour observed between normal and hypothyroid rats.

The first study to be made on the morphology of this region of the brain was concerned with the size and distribution of the pyramidal cells in the lamina ganglionaris (Eayrs & Taylor, 1951), and showed that at both 15 and 24 days old, the density of cell bodies was considerably greater in the cortex of the cretin than in that of the normal rat. The difference was partly due to the fact that the cell bodies of the neurones were smaller in the experimental tissues, but was mainly attributable to a reduction in the growth of the substance intervening between the cell bodies. Subsequent work, directed towards finding which components of this substance were responsible for its reduced growth, showed (i) that there was a mild gliosis in the tissues of the cretins and (ii) that the percentage of tissue occupied by blood vessels in the cortex of the cretin did not differ significantly from that in the normal rat (Eayrs, 1953). It was therefore clear that neither changes in the amount of supporting tissue, nor in vascularity could account for the differences observed in the packing of the neurones. On the other hand hypothyroidism was found to be associated with an appreciable diminution in the number of axons counted in silver impregnated sections. There was likewise a reduction in the density of the dendritic fields associated with the pyramidal cells (Golgi-Cox preparations), for although the number of dendrites arising from the cell body was little changed by the experimental treatment, the cell processes were shorter and branched less in the tissues of the cretins than in those of the normal rat.

It is thus clear that cretinism in the rat is accompanied by a hypoplasia of the cortical neuropil. This implies that the number and pattern of inter-neuronal connections may have been disturbed, a derangement which could have far-reaching significance for the maturation of behaviour.

Maturational Changes in the Central Nervous System

Before attempting to assess the significance of these facts we should first enquire what is the background of structural and functional change in the central nervous system against which the influence of hormones during maturation should be considered. Knowledge in this field is very limited, but it is generally accepted that the

functions of the central nervous system are organised in the form of a hierarchy, the most elementary function in the hierarchy, that involving the reciprocal integration of the activity of neuro-muscular units, being mediated through a system of rigidly organised interconnections. Experiments with the rat involving the cross-anastomosing of flexor and extensor motor nerves have shown that, throughout post-natal life, these interconnections remain undisturbed notwithstanding the severe biological handicap they impose upon the individual (Sperry, 1941). In young amphibian larvae however, an element of plasticity is conferred upon the developing central nervous system, not by biological necessity, but by the "modulation" of neurones, the term modulation implying that as a result of the peripheral connections they make, neurones are able to influence their central inter-connections (Weiss, 1949).

There is little reason to believe that the development of centres "higher" in the hierarchy is governed by factors which differ from those controlling the differentiation and maturation of "lower" centres. Morphological studies show that "higher" centres differentiate later than the "lower," and it is possible that in the rat, at the time of birth, their state of differentiation may correspond with that of the neuraxis of early amphibia. If this be the case, then a prime determinant of the functional connections made by undifferentiated centres may be the modulating influence of the neurones comprising the centres concerned in the next lower function in the hierarchy. Kennard's (1942) work on the infant monkey suggests that such a state of morphological plasticity, during which unusual connections may be established, may occur during the post-natal development of the brain of the young primate. A condition is ultimately reached however in the amphibian larva, and so presumably in terrestrial vertebrates, when connections already established become irreversibly fixed and all trace of this form of plasticity is lost.

If this general account of the principles underlying central nervous maturation be valid, then it is reasonable to assume that the role of hormones during the 'plastic' stage of development will differ from that which obtains once the inter-relationship of cerebral centres has become established. In the first instance, it may be anticipated that the endocrine control of behavioural maturation will have a structural

counterpart; in the second, i.e., when basic mechanisms have become irreversibly established, an explanation of the influence of hormones must be sought mainly in physiological terms.

Hormones and Central Nervous Structure

The structural changes shown to occur in the cerebral cortex of the rat as a result of thyroid deficiency at once suggest that the thyroid may be concerned in maturation during its 'plastic' phase. Can these changes be attributed to a specific effect of thyroid hormone on the differentiation of central nervous tissues, or do they arise as a result of more general disturbances in tissue metabolism normally associated with hypothyroidism? On neither of these points is the evidence conclusive. During amphibian metamorphosis, a process which is closely linked with thyroid function, the nervous system becomes modified to fit the needs of reorganised bodily functions. This implies that, in this phylum, thyroid hormone may exert a direct and specific influence on neurone differentiation, but in the hypothyroid rat we cannot, at the moment, be sure that there is more than a gross retardation of a normal sequence of behavioural maturation or that cortical morphology is other than might be expected as a result of such retardation. It is likely, however, that any primary effect of thyroid deficiency is supplemented by indirect influences. For instance, there are changes in the shape of the brain of the cretin which are consistent with its having been distorted as a result of a faulty ossification in the bones of the skull (Eayrs & Taylor, 1951). At the same time the pattern of cerebral vascularity shows that there is a reduction in the number of capillaries and that all blood vessels are dilated (Eayrs, 1943). The picture is one which might be expected to be associated with anoxia, a condition has already been shown to interfere with cerebral maturation (Windle, 1944).

In the maturation of any system whose function is based on inter-connections between its units, significance must be attached to the sequence with which such connections are established. If the plasticity present during the early stages of development is ultimately lost, connections which, for any reason, fail to become established at the proper time may fail altogether, and functions which are mediated through centres which thus get out of step with

the developing whole will be destined never to appear in the behaviour of the individual. Such an explanation has already been suggested to account for the contrast between the apparent irreversibility of the cerebral damage caused by thyroid deficiency in the human cretin and the reversible changes which occur in myxedema. Can the same be said of the rat? Evidence on this point is so far equivocal. The somewhat inconclusive results of Morrison and Cunningham (1941) suggest that medicated cretins are able to acquire a simple conditional response as well as normal rats and better than untreated cretins; and more recently a group of rats made cretinous for the first 24 days of life and later given thyroxin has certainly performed as well on an elevated T-maze as have normal littermates (Eayrs & Lishman, 1953). On the other hand rats, which have been allowed to recover physically from the effects of cretinism have so far failed to solve the 3-table test measuring "reasoning" ability (Maier 1932) or the capacity to delay a response (Hand, 1953), on which normal littermates have given significantly high scores. The rat is a poorly encephalised animal and it is possible that learning a spatial maze is a function which can be executed without recourse to the higher elements of cerebral organisation. It is, however, principally in the use of symbolic processes such as are demanded by abstraction, thought, and reasoning that the human cretin does not respond to replacement therapy. The performance of a delayed response is probably the highest mental function of which the rat is capable, and it may therefore be significant that it is in this capacity that medication has so far failed to restore the cretin to normal.

Facilitation as a Maturation Process

Endocrine influence on central nervous maturation is not, however, confined to the phase during which the primary inter-relationship between neurones is established. For instance the localised application of thyroxin in the vicinity of the 4th ventricle of the mid-larval tadpole will accelerate the final integration of the trigeminal and abducens pathways in the mediation of the lid-closure reflex, although this hormone is apparently without effect until the differentiation of nervous pathways is complete (Kollros, 1943).

The influence of the sex hormones would seem to be one which is confined to the later stages of

central nervous maturation for the neural mechanisms for reproductive behaviour in the rat are bisexually represented and can mature in the absence of the gonads. The interaction between the sex hormones and the maturing nervous system is thus not so much one which concerns the genesis of the two sex-specific neural mechanisms but of the way in which one of these mechanisms comes to be selectively linked with the sex of the individual.

It is possible to account for this phenomenon in terms of the facilitatory effect of androgen on behavioural maturation. The testis becomes responsive to pituitary gonadotrophin earlier than does the ovary (Price & Ortiz, 1944), and the secretion of androgen shows a gradual increase from an early age until well past puberty. By contrast, ovarian activity is characterized by a sudden increase at the time of puberty (Oesting & Webster, 1938). These sex differences are reflected in pre-pubertal sexual activities which are frequently seen in the male but rarely if ever, in the female (Beach, 1942). Hence, although a similar neural network be present in both sexes, the early presence of androgen in the male may, by a process akin to that visualised by Hebb (1949) as underlying the growth of the cell-assembly during perception and learning, establish preferred inter-neuronal pathways. During such a process, androgen could be responsible, by differential action on the enzyme systems concerned in central integration, for an initial and transient facilitation of specific pathways, a more stable engram being later established by growth or other changes. Once laid down, the resistance of such an engram to erasure would confer a sex-specificity upon the nervous system even in the subsequent absence of the gonads.

Beach (1944 b), who has perhaps contributed most to our knowledge of mating behaviour in the rat, has concluded that the facilitatory effect of androgen is concerned with "the integration of separate sensory stimuli into a perceptual pattern," and in this connection has stressed the fact that the cerebral cortex plays an essential part in the mating behaviour of the male, but not in that of the female. It may therefore be significant that experiment has shown that the male is precocious in two forms of behaviour which are cortically mediated, and in a third in which the cerebral cortex is involved to a smaller extent.

The evidence presented here is too fragmentary

and indirect to warrant any far-reaching conclusions concerning the mode of action of hormones on the maturation of the nervous system, and indeed does little more than suggest the general lines of approach to future work. In this connection we may look for two modes of endocrine influence during central nervous maturation: in the first place an influence which governs the morphological and enzymological differentiation of neurones during early development, and secondly a more or less specific triggering action on a pre-differentiated neural network. The available evidence suggests that the influence of the sex hormones may more profitably be studied in the light of the second of these mechanisms, and that while the secretions of the thyroid gland can act in a similar manner, there are good grounds for believing that this hormone is also an important determinant of central nervous organisation.

REFERENCES

- Anderson, A. C. & Patrick, J. R. (1934). Some early behaviour patterns in the white rat. *Psychol. Rev.* **41**, 480-496.
- Beach, F. A. (1942). Sexual behaviour of prepubertal male and female rats treated with gonadal hormones. *J. comp. Psychol.* **34**, 285-292.
- Beach, F. A. (1944a). Relative effects of androgen upon the mating behaviour of male rats subjected to forebrain injury or castration. *J. exp. Zool.* **97**, 249-285.
- Beach, F. A. (1944b). Experimental studies of sexual behaviour in male mammals. *J. clin. Endocrinol.* **4**, 126-134.
- Beach, F. A. (1945). Hormonal induction of mating responses in a rat with congenital absence of gonadal tissue. *Anat. Rec.* **92**, 289-292.
- Beach, F. A. (1948). *Hormones and Behaviour*. New York: Hoeber.
- Beach, F. A. & Holz, A. M. (1946). Mating behaviour in male rats castrated at various ages and injected with androgen. *J. exp. Zool.* **101**, 91-142.
- Benedek, T. & Rubenstein, B. B. (1939). The correlation between ovarian activity and psychodynamic processes. I The ovulation phase. II The menstrual phase. *Psychosom. Med.* **1**, 245-270; 461-485.
- Berg, I. A. (1944). Development of behaviour: the micturition pattern in the dog. *J. exp. Psychol.* **84**, 343-368.
- Bradbury, J. T. & Gaensbauer, F. (1939). Masculinization of the female rat by gonadotropic extracts. *Proc. Soc. exp. Biol. N.Y.* **41**, 128-131.
- Brooks, C. McC. (1933). Studies on the cerebral cortex. II Localised representation of hopping and placing reactions in the rat. *Amer. J. Physiol.* **105**, 162-171.

- Browne, J. S. L. (1952). Effects of ACTH and cortisone on behaviour. *Ciba Found. Coll. Endocrinol.* 3, 197-204.
- Chauchard, P. (1943). Hormones sexuelles et fonctionnement nerveux. *Ann. d'Endocrinologie* 4, 133-134.
- Cleghorn, R. A. (1952). Alterations in psychological states by therapeutic increase in adrenal cortical hormones. *Ciba Found. Coll. Endocrinol.* 3, 187-196.
- Eayrs, J. T. (1951a). The influence of sex on the maturation of the central nervous system in the albino rat. *J. Endocrinol.* 7, 271-279.
- Eayrs, J. T. (1951b). The modification of lactation in the rat by environmental factors. *J. Endocrinol.* 7, 280-287.
- Eayrs, J. T. (1952). Sex differences in the maturation and function of the nervous system in the rat. *Ciba Found. Coll. Endocrinol.* 3, 18-31.
- Eayrs, J. T. (1953). The vascularity of the cerebral cortex in normal and cretinous rats. *In the Press*.
- Eayrs, J. T. & Lishman, W. A. (1953). Unpublished observations.
- Eayrs, J. T. & Taylor, S. H. (1951). The effect of thyroid deficiency induced by methyl thiouracil on the maturation of the central nervous system. *J. Anat. (Lond.)* 85, 350-358.
- Fiske, V. M. (1941). Effect of light on sexual maturation, oestrous cycles, and anterior pituitary of the rat. *Endocrinology* 29, 187-196.
- Hamond, J. & Marshall, F. H. A. (1925). Reproduction in the Rabbit. London: Oliver & Boyd.
- Hanson, D. A. (1949). The influence of age and sex on "reasoning." *J. exp. Biol.* 26, 317-326.
- Hand, N. E. (1953). Thesis for Ph.D. University of Birmingham.
- Hebb, W. O. (1949). The organisation of behaviour. New York: Wiley.
- Herren, R. Y. & Haterius, H. O. (1931). The relation of ovarian hormones to electro-myographically determined Achilles reflex time. *Amer. J. Physiol.* 96, 214-220.
- Kennard, M. A. (1942). Cortical reorganisation of motor functions. *Arch. Neurol. Psychiat. Chicago* 48, 277-240.
- Kollros, J. J. (1943). Studies of the development of the corneal reflex in amphibia. II Localised maturation of the reflex mechanism effected by thyroxine-agar implants into the hindbrain. *Physiol. Zool.* 16, 269-279.
- Maier, N. R. F. (1932). The effect of cerebral destruction on reasoning and learning in rats. *J. comp. Neurol.* 54, 45-75.
- Martins, T. & Valle, J. R. (1948). Hormonal regulation of the micturition behaviour in the dog. *J. comp. Psychol.* 41, 301-311.
- McGraw, M. B. (1943). The neuromuscular maturation of the human infant. Columbia: University Press.
- Means, J. H. (1948). The thyroid and its diseases. 2nd Edition. Philadelphia: Lippincott.
- Morrison, G. W. & Cunningham, B. (1941). Characteristics of the conditioned response in cretinous rats. *J. comp. Psychol.* 31, 413-425.
- Munn, N. L. (1950). Handbook of psychological research on the rat. Boston: Houghton Mifflin.
- Oesting, R. B. & Webster, B. (1935). The sex hormone secretion in children. *Endocrinology* 22, 307-314.
- Pfeiffer, C. A. & Hooker, C. W. (1942). Experiments on the source of ovarian androgen in the mouse. *Anat. Rec.* 83, 543-571.
- Price, D. & Ortiz, E. (1944). The relation of age to reactivity in the reproductive system of the rat. *Endocrinology* 34, 215-239.
- Rowan, W. (1931). The riddle of migration. Baltimore: Williams & Wilkins.
- Small, W. A. (1899). Notes on the psychic development of the young white rat. *Amer. J. Psychol.* 11, 80-100.
- Sperry, R. W. (1941). Effects of crossing nerves to antagonistic muscles in the hind limb in the rat. *J. comp. Neurol.* 75, 1-19.
- Thomson, A. P. D. & Zuckerman, S. (1953). Functional relations of the adenohypophysis and hypothalamus. *Nature* 171, 970.
- Tilney, F. (1933). Behaviour in its relation to the development of the brain. Part II. Correlation between the development of the brain and behaviour in the albino rat from embryonic states to maturity. *Bull. Neurol. Inst. N.Y.* 3, 252-358.
- Wang, G. H. (1923). Relation between "spontaneous" activity and oestrus cycle in the white rat. *Comp. Psychol. Monogr.* 2, 6.
- Weiss, P. (1949). Experimental analysis of co-ordination by the disarrangement of central-peripheral relations. *Symp. Soc. exp. Biol.* 4, 92-111.
- Windle, W. F. (1944). Structural and functional alterations in the brain following neonatal asphyxia. *Psychosom. Med.* 5, 155-156.
- Zuckerman, S. (1953). *Biol. Rev. In the Press*.

The Use of Cats in Farm Rat Control

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Introduction

Although cats are very often kept on farms and other premises, there is much difference of opinion about their efficiency in keeping down rat infestations. Many farms have been seen where cats live in company with permanent rat populations, often of some size: and others where it is claimed that cats are responsible for rat scarcity. The difference is usually attributed to the more efficient behaviour of some cats as rat catchers, either by constitution or training. The present report contains some definite evidence on the subject, collected in the course of field research into the ecology of rat populations formerly inhabiting the Agricultural Council's estate on the Downs at Compton, Berkshire. It is not claimed that these facts form more than a contribution towards a rather complex subject, on which very little scientific information exists. My own detailed notes cover the period from the winter of 1939-40 until the summer of 1942. A. D. Middleton's further general observations showed no further change in the cat-rat situation up to at least the spring of 1945.

The late Dr. G. Dunkin, while Director of the Field Station at Compton, took a particular interest in the use of cats for rat control, and it is as a result of his successful experiments in introducing cats onto the farms there that the present observations were made. The full facilities and co-operation given by Dr. Dunkin and by the Farm Manager, Mr. E. A. MacMillan, are gratefully recorded. This research formed part of a war-time investigation done by the Bureau of Animal Population under the auspices of the Agricultural Research Council, for whom a report was originally prepared in December, 1943. The following account includes some assessment of the population sizes, because the behaviour of cats as rat-destroyers is evidently related in part to relative population densities of the two species.

Field Observations

From December 1939 until 1945 close observations were made at Compton, including records of corn-rick rat (*Rattus norvegicus* Berkenhout) populations obtained at threshing

during three seasons, various experiments in rat control, and notes on the ecology of the rats on the estate generally. Five farms and one cottage are considered below.

Manor Farm. In the central village area, and not much studied, as it is not an isolated set of premises. No severe rat infestations were ever reported in 1939-45. In September 1942 there were about four cats.

Superity Farm. A dairy farm about 900 yd. north of the village, with arable and pasture fields, and with several cottages near. The man in charge said there had been a dynasty of cats here since at least 1918, and that the farm buildings had always been rat-free except for occasional visitors. A careful search in March 1940 revealed no traces of rat occupation anywhere in the premises, except for one small hole in a calf stall, which later became inactive. Corn-ricks within 50 yd. were very lightly or not at all infested; but this may have been wholly or partly due to the seasons at which the ricks were threshed. Those further to the north had in some instances heavy infestations. The following figures are for all ricks on Superity Farm area, for three seasons. They represent rats classified in the fields as "active" i.e. young nestlings are omitted.

Season 1939-40. 4 ricks within 50 yd. of the farm, threshed in October, had 0, 0, 6, 9 rats. 6 ricks further away, threshed in July-September 1940, had 67, 50, 0, 0, 0, 0 rats. *Season 1940-1.* There were no ricks near the farm, but outside a 50 yd. radius 7 ricks threshed in October 1940-April 1941 had 6, 0, 0, 24, 19, 2, 155 rats. The last was in a Dutch barn built in 1940, lying about 650 yd. from the farm buildings. *Season 1941-2.* Two ricks near the farm threshed in May, 1942, had no rats. 5 others more than 50 yd. away, threshed April-May 1942, had 0 (two ricks), 10 (two ricks), 47, 97, 16. All these rats were from the Dutch barn, at which poison baiting produced the figures of 47 and 16, the rest being killed during threshing. The numbers are therefore underestimates, as they do not allow for rats dying of poison below ground or in other cover. No poisoning or trapping was done on

any part of this farm area during the first two seasons.

To sum up: 15 rats occurred in 6 ricks within 50 yd. of the farm buildings, and at least 493 in the 20 ricks further away. Thus the Dutch barn evidently gained no effective rat control from the cats. In the winter of 1939-40 there were at least five cats at the farm, but in November 1944 there were only three, owing to losses. from feline distemper. In addition there were several in cottages close by, though it is uncertain whether these hunted on the farm premises.

Ilsey Down Farm. Also a dairy farm about a mile north-west of Superity Farm, with pasture on most sides, but situated not far from the village of East Ilsey. The man in charge reported that about 1938 there was a severe rat infestation, over 60 rats being killed (partly by gassing). Cats were introduced after this, and there had been no trouble since. In November 1941 a careful search showed no rat traces of any kind. The buildings were not very modern, and woodwork still showed the traces of earlier rat gnawing. There was plenty of food and cover for a rat population. One rat had been killed by a cat the day before this inspection, and this was said to be the first observed for a year. About three cats present. (Until the autumn of 1941 no corn ricks existed on this farm. Four ricks situated some 250 yd. away had no rats in when they were threshed on 26 February-2 March and 10 April 1942).

Cheseridge Farm. Another dairy farm, about a mile south-west of the village of Compton, in a fairly isolated position, with arable land and woods near, and pasture immediately adjoining. In the winter of 1939-40, members of the Bureau studied a very severe infestation of rats that were destroying sacks of cattle food: from June to December 1939 some 105 rats had been killed by gassing and 30 by break-back traps. Until the end of December there were no cats. Then a single cat was introduced. The cowman watched it with rats running past, making only feeble efforts to attack them, and it was not seen to have caught any during the first fortnight of its residence, while the infestation was still high. During January to March 1940, control efforts (including poison baiting) by D. H. Chitty resulted in an almost complete reduction of the rat population, which was followed up by careful sealing of rat holes and the introduction of more cats. In mid-June there were six cats.

The farm premises, including dairy buildings, manure pit, Sisal-kraft silo and Dutch barn, were now almost completely rat-free, though all these and an adjoining pit had been infested previously. This fact was proved by reports from the man in charge, and by several careful surveys. Damage had diminished from something like half a sack of cattle food per week to nil. Some of the cats appeared to be much better ratters than others; nevertheless by July the original cat had begun to kill rats in the neighbouring cottage gardens, and bring them to its kittens. In the following month, only four rats were known to have been killed on the premises, and no others seen. In early October 1941, it was reported that no rats were ever seen to enter the premises, which inspection showed to be clean and free from traces. Various cats were seen lounging about: in December there were at least four. In this month the oats rick in the farmyard Dutch barn was threshed and there were no rats.

Meanwhile, rats continued to haunt the gardens of two cottages adjoining the farm premises, and the banks of a lane leading down from the farm to some woods. In October-November 1941 at least ten rats were killed by poison baiting in the gardens and lane. At this time the farm buildings were still quite rat-free. In September 1942 there were five farm and three cottage cats.

Rats continued to infest corn-ricks not very far away. The records of rats killed in these ricks are given below: they include some for Hill Barn, a large isolated barn, with associated groups of field ricks and a field cattle byre, situated about 600 yards from Cheseridge Farm. Hill Barn did not have any human or resident cat population.

Season 1939-40. No ricks close to the farm. 5 ricks in the Hill Barn area, threshed February 1940, had 112 (Hill Barn), 8, 12, 14, 9 rats. *Season 1940-1.* One rick in the farm yard, threshed December 1940, had no rats. Two ricks about 125 yd. away, threshed October 1941 (operations were extremely late on many ricks from the previous year) had 4, 34 rats; one about 250 yd. away, threshed April 1941 had 32 rats; Hill Barn had no grain in this year; 7 ricks from the Hill Barn area threshed July-December 1941, had 0, 0, 0, 129, 15, 62, 0. *Season 1941-2.* No ricks near the farm. Hill Barn had 229 rats in February 1942; two ricks in the same area, poisoned at the end of May and threshed about a week later, had 15 and 6 rats.

To sum up: the only rick in the farm yard had no rats. 18 ricks more than 50 yd. and mostly more than 250 yd. away had 681. These observations, and the ones for Superity Farm already mentioned, show particularly clearly how local any influence of the cats is.

Cowman's cottage. The cowman of Cheseridge Farm, whose isolated cottage lies by the road half-way between there and Mayfield Farm, had an infestation of rats in 1937-38, which came from ricks near the road opposite his cottage. He got rid of the rats and put in a cat immediately afterwards. This cat was sometimes seen hunting by the ricks 180 yd. from the cottage. There was little or no further rat trouble at the cottage, in spite of the existence of some heavy rick infestations not far away.

Season 1939-40. Two ricks across the road from the cottage, about 150 yd., threshed December 1939 had 58, 77 rats. *Season 1940-1.* Three ricks 3-400 yd. away, threshed February-April 1940 had 8, 2, 32 rats. *Season 1941-2.* Two ricks about 180 yd. away, threshed January-February 1940, had 53, 22 rats. *Total:* 7 ricks with 252 rats.

Mayfield Farm. This is a pig farm on the outskirts of the central village of Compton. In 1939-40 onwards it had severe infestations of the whole premises, including one fairly modern pig-house, the meal-mixing barn, pump-house, ricks in the farm-yard, drainage system, manure heap, and moveable pig pens in the field close by. The complete story of attempts to clear the farm of rats is a complicated one, as various different experiments were involved, and therefore only some examples of the numbers of rats destroyed will be given. No cats had ever been induced to stay permanently on this farm, partly owing to the presence of two dogs. The farm was virtually free from the influence of cats, although there were some kept in cottages not far away.

Farm-yard ricks: One threshed November 1939 had 57 rats, one threshed in December 1940 had 60, one threshed in December 1941-January 1942, had 35. *Gassed, etc., on premises:* over 110 rats in winter, spring and summer 1939-40, 44 in winter and spring 1940-1, 13 in winter and spring 1941-2. *Killed under moveable pig pens in field close by:* 122 old and young rats, April 1940. *Total:* over 441 rats in and close to the farm premises.

Other instances. There are no other instances

recorded in the Bureau's files that provide the same amount of detailed evidence as the Compton farms; but the following are suggestive of the ability of cats to maintain farms rat-free, in some cases after preliminary clearance by other means.

- (1) In 1942-5 A. D. Middleton carried out a successful block control campaign against rats on an area of 11,450 acres that included the Compton Estate. Of the 34 farm "units" serviced (which included outlying barns etc), 14 had been practically free from rats at the start in 1942. These included four Compton units already mentioned. Five of the remaining ten had cat populations, three were catless but not suitable for permanent rat colonies, one had dogs but no cats, and on the tenth the absence of rats was inexplicable. He also noted that 6 of the 20 infested units were farms with numerous cats. In summing up his experience here, he says: "With the possible exception of one locality (which has one cat), most of the units on the Compton area which had regular food supplies and few or no cats, were rat infested."
- (2) Mr. W. D. Hollis wrote to me (9 March, 1940): "I always have to keep at my house [in Hampshire] three or four cats, otherwise rats immediately invade the premises and eventually get into the house. Last autumn I had stored in the barn close to my house over 600 sacks of corn and a considerable amount of cattle food, and my men remarked when this barley was sent to the maltsters that not a sack was touched." The estate in question was rat-infested, no poison being used.
- (3) A small farm near Oxford was well infested in October 1942, and completely cleared of rats in the course of poison baiting by the Bureau. *There had been one or two cats there before*, but the farmer got a few more. He fed them on milk only. In October 1943 the farm was still completely rat-free as searching for traces proved.
- (4) Another farm not far from the last one was taken by the farmer over eight years before, when it was in a very dirty and rat-infested state. He killed most or all of the rats with ferrets, dogs and traps, moving the existing cover, and thereafter introduced several cats—on the average about six. This solved the rat problem.

Relation Between Cat and Rat Populations

The main evidence about the effect of cats on the Compton rat infestations is seen to be of two kinds: (a) four out of five farms, and a cottage, that had cats installed remained almost completely free from rats, after these had, in at least three cases, been initially destroyed by other means; while the farm that had no cats continued to suffer from recurrent infestations. (b) Ricks in the fields around, in some cases quite near, the premises with cats continued to have quite heavy infestations; while two field barns 600 and 650 yd. from the nearest farm, had extremely heavy infestations in every season that they contained corn-ricks. I have no facts to show that cats can by themselves ever control and exterminate a large rat infestation. They certainly do not do so in some instances, so that the introduction of cats as an initial clearance method is at least uncertain. It has been shown that the zone maintained free of rats by the cats is a restricted one, and that they evidently have little influence on field rat populations, in so far as corn-ricks are an index of the presence of these generally on the farm. On this point, there was plenty of proof that practically all the rats on the Compton estate went into the ricks or the farm buildings in winter, although a small number continued to run in the hedges (as shown by rats caught in tunnel-traps and rabbit-traps). Although it is clear that cats do not control the rats in field ricks, the evidence suggests that they can keep farm-yard ricks clear as well as the buildings etc.

The following explanation is suggested of the ability of cats to keep a clear zone round the farm buildings, when once the infestation of rats has been removed. It seems quite possible that the predator-prey balance between thoroughly established cat and rat populations, each fully conditioned by experience to the local cover complex, is quite different from that between an established cat population subsidized by human or animals' food, and single rats arriving from the fields to enter an unfamiliar environment. The difference would be analogous to that between police and criminals permanently inhabiting a large town which they both know thoroughly, and the arrival of an enemy parachutist in an area full of Home Guards conversant with the ground. What is known about the reactions of *Rattus norvegicus* towards new spatial arrangements, new objects, and new

food sources, supports the notion that any rat arriving on a farm strongly held by cats would at first be more highly exposed to risk. There is a slight suggestion from the story of Cheseridge Farm that once such a farm becomes clear, very few rats enter the area watched by cats, even though abundant food and cover remain, but more exact observations would be required to establish this point. The final test required for the theory that cats can usually only keep a farm clear if it has been first thoroughly cleared of rats, would be to install four cats on a moderate-sized rat-infested farm, and leave it for six months with no other form of control.

The paper by Kuo (1930) is the best record I know of exact observations by a comparative psychologist on the development and variability of the rat-killing habit in cats. Of 20 kittens reared alone, only 9 killed rats or mice without any training. 18 out of 21 kittens brought up in an environment where killing was going on, killed rats or mice before they were four months old. Three out of 18 kittens raised with cage rats as mates killed rats, but not their actual mates. Nine out of 11 non-rat-killing cats placed in an environment where rats were being killed, soon became rat-killers. Hunger was not a factor in rat-killing: cats conditioned to being vegetarian killed rats but mostly would not eat them. These results rather suggest that partial feeding of farm cats keeps them anchored to the farm, and at the same time induces enough searching activity to bring the cats in contact with the rats. It is, of course, known that some cats eat the rats they catch.

It is generally believed that the quality of particular cats and their offspring is the explanation of different degrees of efficiency in rat-killing. There is no doubt a certain amount of truth in this idea. But the Compton cats were not selected especially for their ratting qualities: indeed Dr. Dunkin got some of his by simply advertising for "a hundred cats." Some of these, it is true, came from a farm at a neighbouring village, in a heavily infested district and this farm had always kept cats and was markedly rat-free. It seems probable, however, that the number of cats is just as or more important than their quality, and that, given a cleared set of premises, almost any cats will be efficient provided they are induced to remain there by feeding, and that at least three are kept on an ordinary-sized farm.

Relative Efficiency of Cats and Human Beings in Rat Control

In the following discussion, I shall assume that the condition described for the Compton farms may be applicable to at least a large number of other dairy farms in the country. Under "efficiency" we have to consider not only the actual success of the cats in exterminating or controlling rat populations, but whether the cost of doing so, both in food and labour, is low enough to justify their use; and we must not forget also that cats have other influences on pests and on wild life generally that may have to be reckoned in the account.

If cats destroy every rat soon after it arrives onto previously cleared premises, they are certainly more efficient at killing than human operators, since the rat population has time to build up in the intervals between service treatments. Cats carry out this control without the necessity of laying poison baits, or of gassing, so that there is less risk to life and health of domestic animals and birds. And the killing efficiency of human operators is very seldom 100 per cent. Cats are therefore better rat controllers, within the two conditions that they do it around farm buildings, and that they are not expected to tackle a large initial infestation.

As regards the cost of keeping cats, Dr. Dunkin estimated that each Compton farm cat was given about half a pint of milk per day, which is 23 gallons per year. This milk represented about a third of their daily needs in food. (Sometimes the cats had bread and milk, but this factor is ignored in the present discussion). A rough calculation suggests that, on a calorie basis, a population of four cats on a farm would consume at least five times as many calories in the food supplied to them as milk, as the total calorie requirements of two human operators doing a total of 12 man-days treatment a year. This figure for the operators assumes the maximum time likely to be needed, and would be probably lower in practice, since the number of treatments is usually adjusted nowadays to the severity of the infestation and re-infestation.

Rats do structural damage and carry diseases, as well as destroying human food. Control is also an insurance against higher infestations, and the difference between the cost measured in food values between cats and human operators might be negligible when compared with the losses that a failure to control rats might entail.

It would seem best therefore to regard cats as a useful source of additional farm labour, since we live in a period of full employment and general shortage of skilled labour. To the extent that they keep farm premises clear of rats, they can reduce the labour required for periodic servicing of the whole farm.

As regards the relative costs of maintaining cats or hiring service operators, it is difficult to make calculations that are in any way reliable. Theoretically it can be done by comparing the wholesale milk costs of what the cats are given, with the contract costs of county pests organisations. But the latter vary so much that exact comparison is impossible. The difference between the two sets of costs does not, upon the whole, appear to be very large. Incidentally, the cost of cats' food also covers that of their transport on their four feet.

Cats have a great advantage over human beings in the control of rat populations at a very low level: they do not seem to get bored! The psychological problem of such maintenance work may to that extent be helped.

Summary

1. Four out of five farms and a cottage on a downland area in Berkshire, on which cats were installed, remained almost completely free from rats after the latter had in at least three cases been initially destroyed by other means. The other farm, that had no cat, suffered recurrent infestation. Ricks more than about 50 yd. from cat-occupied units continued to have rat infestations, often heavy ones.
2. From these and certain other instances, it is concluded that if a sufficient number of cats (say, four) is introduced after complete rat extermination has been done, and if part of their food is supplied as milk, they will maintain the immediate area of the farm buildings rat-free. They will not necessarily clear a farm of an existing rat infestation. The quantity of cats is probably more important than their quality.
3. To keep cats on this scale is certainly more expensive in human food (used for the cats), than if human servicing was used for rat clearance, but it supplies a useful and efficient source of additional labour, which has the important attribute of maintaining the efficiency of control at very low rat densities.

REFERENCE

- Kuo, Z. Y. (1930). The genesis of the cat's responses to the rat. *J. Comp. Psychol.* 11, 1-35.

The Grazing Behaviour of South Devon Cattle Under Experimental Conditions

By R. J. HALLEY

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Grazing behaviour studies were made upon South Devon cattle at The Seale Hayne Agricultural College during the summer of 1950. They constituted, however, only part of a larger study upon the effect of the stage of maturity of a sward upon milking cows. The aspects of behaviour studied were those of grazing and lying down. The times spent performing both these actions were recorded to the nearest one minute during daylight and to the nearest five minutes during darkness.

The experiment was laid out in the form of a 4×4 Latin Square. The four treatments were swards at different stages of maturity, obtained by cutting the plots at varying intervals of time before grazing the experimental area. Eight cows were employed in the experiment, two cows grazing one plot representing each treatment during each observation. Each plot was an eighth of an acre in size and was grazed by one pair for twenty-four hours, regardless of the amount of grass present. Two complete observations, each consisting of four twenty-four hour observations were conducted during summer of 1950. In the first series of observations the cows received no extra hand feeding. However, in the second series of observations each cow received 3 lb. per day of a concentrate ration balanced for milk production.

Experiment I

Table I shows the method of producing the

four different swards by cutting, the weight of grass dry matter available per acre, the time spent grazing and the time spent lying down. The results show that as the age of the sward increases the weight of grass available increases. The grazing behaviour of the cows varied as the age of the sward increased—grazing time decreasing and lying down time increasing. The differences produced by the treatments in the time spent grazing and lying down, however, were not sufficiently large to be significantly greater than the error contained in the experiment. The large error contained in the experiment—Error per cent 10 per cent—may, in part be explained by the fact that one of the cows went lame during the experiment at a stage too late to have her replaced. Botanical analyses were not made on the herbage which, with all treatments, had the appearance of an all grass sward dominated by perennial ryegrass.

Experiment II

Table II shows the method of producing the different swards, the weight of grass dry matter available per acre, the time spent grazing and the time spent lying down in the second experiment. In this series of observations the pasture treatments produced significant differences in the times spent grazing and lying down. With Treatments II, III, and IV, respectively, the time spent grazing decreased and time spent lying down increased as the age of the sward

TABLE I.

Treatment	Date of Cutting	Average No. of days before grazing	Tons of D.M. available per acre	Grazing time minutes	Lying down time minutes
I	Not cut		1.5	343	644
II	27th March	34	1.0	354	608
III	3rd April	27	0.7	392	590
IV	10th April	20	0.5	406	585
Proportion of time between a.m. and p.m. milkings				40%	30%

TABLE II

Treatment	Date of cutting	Average No. of days before grazing	Tons of D.M. available per acre	Grazing times minutes	Lying down time minutes
I	10th July	69	1.2	400	636
II	31st July	48	0.6	370	652
III	14th August	34	0.4	425	606
IV	28th August	20	0.3	448	572
Significant differences at 5% level of significance				34	52
Proportion of time between a.m. and p.m. milkings				43%	26%

being grazed increased. However, the times spent grazing and lying down with Treatment I fell between the results for Treatments II and III. The error contained in the second experiment—Error per cent 5 per cent—was considerably less than the error contained in the first experiment.

Distribution of Grazing and Lying-down Time

Tables 1 and 2 also show the distribution of grazing and lying down time between milking periods in the two experiments. In the first experiment forty per cent of the grazing time and thirty per cent of the lying down time fell in the interval between the morning and evening milkings. In the second experiment the figures were 43 per cent and 26 per cent respectively. Distribution of grazing and lying down time did not appear to be influenced by the pasture treatments in either experiment.

Discussion

The average time of 6.54 hours spent grazing obtained in the present experiments is very close to earlier results (i). However, the average time spent lying down of 10.26 hours is about

one hour longer than the results given in (i). It appears, therefore, that the grazing behaviour of the very heavy South Devon Cow (12½ to 13 cwt.) is not markedly different from that of other lighter breeds of cattle.

The experiments show that certain aspects of behaviour vary with the pasture being grazed; and also that these variations can be measured with sufficient accuracy to be of significance. The effect of increasing the maturity of a sward is to increase the weight of grass available and secondly to alter the quality of the herbage available. In the first experiment the herbage on all treatments was almost pure grass. However, in the second experiment the proportion of clover (red clover) present increased with the age of the sward. This obvious change in quality from treatment to treatment in the second experiment, probably explains the unexpected behaviour of the cows while grazing Treatment I, where there was a high proportion of red clover in flower.

Acknowledgments

The author wishes to thank Dr. H. I. Moore for his helpful criticism and advice.

Symposium on Rat Behaviour

This Symposium was held in the Department of Psychology, Birkbeck College, Malet Street, W.C. 1, on Thursday, 9th, and Friday, 10th July, 1953, under the auspices of the Association for the Study of Animal Behaviour. Abstracts of the papers presented are given below.

HORMONES AND CENTRAL NERVOUS MATURATION, WITH SPECIAL REFERENCE TO THE RAT

By J. T. EAYRS

Department of Anatomy, University of Birmingham

The responses of an organism to changes in its environment are, for the most part, mediated by the integrated activity of two systems, the nervous and the endocrine. The interaction between these two systems in the mature individual may take one of several forms: (i) the activity of the nervous system may be modified as a result of the secretion of hormones; (ii) the nervous system may exercise a control over the body's metabolic processes by stimulating the release of hormones or even by acting as an endocrine organ itself; or (iii) both modes of interaction may be combined to provide essential links in a chain of reactions constituting a total behaviour pattern.

The fact that both systems develop side by side in an orderly manner suggests that their close inter-relationship may be laid down during ontogeny. This possibility has been studied in relation to the secretions of the gonads and of the thyroid gland.

Gonadotrophic hormone precipitates sexual maturity when administered to infant rats, for not only do the reproductive organs develop precociously but this process is accompanied by the simultaneous appearance of mating behaviour. Complex behaviour is built up from simpler components, and it is therefore reasonable to suppose that simple automatic behaviour might likewise be advanced by stimulating the secretion of the sex hormones. An experimental analysis of such behaviour suggests that the functioning of certain postural co-ordinating centres is accelerated by the secretion of androgens and that this facilitatory process may extend to higher forms of behaviour.

The overt effects of thyroid deficiency in central nervous development and function are

well known in man, and the view that the cerebral changes associated with untreated cretinism are irreversible has been widely accepted. There are several ways of making rats cretinous and some of these have been used to study the effect of early thyroid deficiency on cerebral maturation. Experiments show that a gross retardation in the appearance of automatic behaviour is associated with marked changes in the shape of the brain, and in the structure and vascularity of the cerebral cortex. Observations made during experiments still in progress suggests that, in the rat, replacement therapy may restore both behaviour and cortical structure to normal.

Two main hypotheses may be advanced in relation to the mode of interaction of the nervous and endocrine systems during maturation. In the first place, it may be postulated that a newly secreted hormone acts on a pre-differentiated nervous mechanism which is genetically determined and which develops independently of the endocrine organ ultimately destined to activate it. Alternatively, or perhaps in addition, endocrine secretions may themselves exert a trophic influence on nervous maturation. In the case of the steroid hormones the first of these mechanisms would seem to be the more important, although there is some evidence that androgens may act as a stimulus to maturation. Thyroid hormone, on the other hand, although it may facilitate the functioning of quite specific centres, exerts an undoubted influence on central nervous maturation. Whether this influence is a primary one, or is mediated secondarily through the action of thyroid hormone upon other tissues, is a problem which cannot be decided on the basis of the present somewhat limited evidence.

PROBLEMS OF FOOD SELECTION BY RATS

By S. A. BARNETT

Department of Zoology, University of Glasgow

Rats faced with a choice of foods may (1) show preferences which are general in the species or variety regardless of environmental differences. Among such preferences are, for instance, those of the wild rat (*Rattus norvegicus*) for sweet rather than non-sweet mixtures, and for foods containing no aniseed oil rather than those which do contain it. Responses to flavours, and to the mechanical properties of foods, seem often to be of this kind.

For a wide range of foods, however, choice is determined to an important extent by (2) the experience of the individual. The sorts of individual experience which influence selection are very diverse: they may have (a) a relatively long term effect, or (b) a momentary one.

(a) Among long-term effects those of (i) the physiological properties of foods have been much studied. Albino rats can select the nutritionally better of two foods in some circumstances. Wild rats reject foods containing poison which have previously made them ill. This poison-shyness has been studied quite independently of the work on dietary self-selection, but is evidently one aspect of a general ability to respond to the physiological effects of some food materials.

Another fairly long-term effect is that of (ii) habit or familiarity. Wild rats accustomed to one food may continue to eat mainly this food for some time after another (normally preferred) becomes available.

(b) Examples of momentary effects are those induced by other rats. There is no evidence for systematic social co-operation in wild rat colonies, but one member may (i) benefit incidentally from the activities of others, especially from the carriage of food into the nest. In such a case food choice is made by proxy, but what effect it has on subsequent foraging is unknown. (ii) Young wild rats beginning to venture outside the nest tend to follow or to orientate themselves on the mother (taxis component ?); she may thus lead them to food, but there is no evidence for detailed imitation. Where there is crowding at a feeding point larger rats tend to drive others off.

Rats quickly learn to eat foods of great diversity, in any place they can reach. The versatility they display depends on (a) their generalised ability for associative learning; (b) their highly developed tendency to explore their environment and to sample everything in it.

CONVULSIONS IN THE NORMAL BEHAVIOUR OF RODENTS

By M. R. A. CHANCE,

Department of Pharmacology, University of Birmingham

Changes in the amount of glycogen and lactate occur in the brain of the mouse as a result of applied stimuli. Lactate increases with the intensity of the stimulus, but glycogen rises only when these stimuli produce convulsions. In this sense, a rise in brain glycogen reflects convulsive activity in the brain.

Estimation of the glycogen in the mouse brain immediately following different types of normal behaviour shows that during some types of activity a glycogen increment occurs, and that during others it is absent.

A study of the physiological influences capable of raising the brain glycogen in the resting mouse revealed that a rise in blood sugar or an injection of anti-insulin hormone

(from ox pituitary) are two factors which, acting separately, can induce a glycogen increment. The extent of the rise, however, is insufficient to account for the increments recorded during some types of normal behaviour. Moreover, those types of behaviour which bring about a glycogen increment are not, in every instance, accompanied by a rise in blood sugar. Conversely, a rise in blood sugar may occur without a rise in brain glycogen.

It is concluded, therefore, that since some types of normal behaviour are associated with a glycogen increment such behaviour is of a convulsive nature. An analysis of these types of behaviour supports this conclusion. For example, the falling posture adopted by a mouse, when

its support is removed, can be shown to protect it against the haemorrhage which would result from concussion at the end of a fall. The posture appears within a fraction of a second, and so does the glycogen increment. The rigidity of the limbs and trunk suggest that many muscles participate in maintaining the posture, and that, therefore, not only a maximal rate of discharge, but multi-motoneurone discharge may be involved.

The fact that convulsive discharge occurs in a fall and during a jump suggests that other types of behaviour, which are already recognised to be convulsive, might profitably be regarded as being part of the repertoire of the animal's behaviour. Audiogenic hyperexcitement may be an instance of this, since it can be shown that, except in the terminal phase, the animal relies in this sequence of behaviour on the release of mid-brain co-ordinating centres to structure its behaviour. It is suggested that this is a type of emergency reaction appropriate to the situation in which there is a complete absence of clues as to the appropriate response. In these

circumstances, *Peromyscus* exhibits an excessive flight reaction followed by aggressive saltation, and the sequence of acts ends in cataleptic postures.

The fact that recognisable convulsions accompany or follow orgasm in a high proportion of men indicates clearly that, even in ourselves, this type of nervous discharge should not in itself be regarded as a pathological disturbance of the nervous system. It is much more readily understood as a manifestation of a generalised release of the lower motor centres from cortical integration.

From this point of view, the volume of work already brought forward to show that audiogenic seizures are likely to occur in animals suffering from a variety of semi-pathological or pathological conditions is not evidence in itself that this mode of discharge is always pathological, but rather that this type of nervous activity can be initiated both by pathological causes, and as a normal response to circumstances met with in the life of the animal.

THE VISUAL WORLD OF RATS

By IAN M. L. HUNTER

Oxford

A general survey of the visual world of rats involves consideration of the part played by vision in these animals' various activities. Of these activities, spatial adjustment and orientation has lent itself most readily to laboratory investigation. Honzik and others have shown that, for normal rats learning an elevated maze, vision is the dominant sense, with olfaction of secondary importance and the other senses of negligible significance. In blind rats, olfaction is of major importance. In blind-anosmic rats, audition enables learning to occur. Rats deprived of vision, smell, and hearing show almost no signs of learning. While normal rats use both intra-maze and extra-maze visual stimuli, the latter are especially important and it has been found, in situations other than the elevated maze, that the rat's visual world is dominated by the more distant, and more stable, features of the environment. In the enclosed maze, vision is less important because fewer visual stimuli are present. Here taction seems to play some part, the walls providing stimulation of the rat's vibrissae, nose, and sides. Crozier & Pincus have demonstrated negative phototropism in young rats with eyes unopened.

Beach finds that the usual stimulus for the male rat's mating behaviour is a combination of visual, olfactory, and tactual stimuli provided by the female. Vision, however, may be removed without eliminating or altering mating behaviour, but, at the same time, vision may enable mating to occur in the absence of olfactory and tactual stimuli.

By using specially designed discrimination apparatuses, it has been shown that rats can react to red light according to its wave-length and that brightness, pattern, and size vision is good.

The fact that the rat reacts to certain environmental features more readily than to others, led to the suggestion that discrimination learning involves trying out a succession of hypotheses until the correct one is hit upon, i.e., involves reacting, now to this selected set of characteristics, now to that, and learning meanwhile nothing about those characteristics "not attended to." But experiments discredit this view, and reveal that, while rats are apparently reacting to a particular aspect of the stimulus situation, differential learning is taking place with respect to other stimulus aspects (pro-

vided that the rat is actually being stimulated by them). In general, it seems to be the entire discrimination situation to which rats react since changes in even its non-differential features often produce discrimination breakdown.

In brightness and in size discrimination, rats react, depending on circumstances, to either the relational or absolute features of the stimulus pair, e.g., to either the brighter of two stimuli or to a stimulus of particular brightness. Relational reactions are favoured by (1) increasing similarity of the members of the train-

ing pair, (2) increasing similarity of the test pair, as a whole, to the training pair, and (3) within limits, increasing amounts of practice with the training pair. The mechanism of relational discrimination is not yet understood.

It may be concluded, in the words of Lashley, "that the rat's visual system functions most efficiently in spatial orientation—the recognition of relative distance and direction—and that the identification of objects or forms, though possible, is secondary to a system of space co-ordinates."

STEREOTYPE BEHAVIOUR IN THE RAT

By R. H. J. WATSON

University of London

The study of abnormal behaviour patterns in animals is receiving increasing attention. As in most animal psychology a considerable amount of it has been done on rats. The work done on stereotype behaviour in particular indicates the difficulties in arriving at a satisfactory definition of "abnormal." Various interpretations of this concept are considered. One such interpretation was that formulated by Maier, who, on the basis of his experiments on stereotype behaviour in rats developed in an "insoluble problem," suggested that abnormal behaviour could be differentiated from normal behaviour on the grounds that abnormal patterns did not conform to predictions from learning theories whereas normal behaviour

did. He therefore postulated two qualitatively different forms of behaviour; one instigated by normal motivational forces and the other developed under frustration. Later work has cast some doubts on the validity of this hypothesis. Details of a research project involving a more complex "insoluble problem" and a correspondingly more complex stereotype pattern in rats will be given. The analysis of the results indicates that both in the "insoluble problem," and in a subsequent "soluble problem," the behaviour of the rat conforms in a number of criteria to that which would be predicted from conventional learning theory. The results also suggest that such stereotypes would tend to be self-perpetuating.

RESPONSE PATTERNS IN THE RAT

By H. M. B. HURWITZ

Department of Psychology, Birkbeck College, University of London

The laboratory rat has made a highly satisfactory subject for experiments on the learning process. Generally speaking, present day research in this field seems to be concerned with two closely related problems: specification of the factors which play a role in the learning process (including their functional inter-relationships) and their quantitative description.

In this connexion, it is commonly assumed that the rat's behaviour may be analysed by

reference to two primary factors: drive and habit. Thus the magnitude or strength of a given response is assumed to be a function both of the intensity of the drive which activates it and of the strength of the habit previously formed. The Skinner-box—a 1 ft. square box fitted with a food or water delivery apparatus which is operated by a lever—is the favourite experimental device used in studies having as their object the determination of the relative

roles of these two primary factors. At first the animal is trained to operate the lever in order to obtain a small quantity of food or water. An "experimental extinction" procedure is then followed, during which the reward is withheld and a count made of the number of lever pressing responses given within a fixed period. Responses performed under these conditions form the basis of the theoretical ventures of Hull and his school, and the less ambitious parametric investigations of Skinner.

An alternative way of looking at the rat's behaviour is to record changes in the *pattern* of responding, during training and experimental extinction trials. Instead of recording only the frequency of lever-pressing, as previous workers have done, it is possible, in addition, to record

the activity of the rat at the food trough together with the time intervals between lever-pressing and eating. An analysis may then be made of the changes which occur in the timing and serial order of the selected events, and their respective duration and intensity. Experiment on these lines which have been conducted for the past year, have yielded interesting information about the patterning of these responses. It would seem that the rat's behaviour under extinction might be best explained by postulating a secondary drive, "frustration," which operates when reward is not obtained at expected times. Evidence for the conjoint operation of the primary drive (hunger or thirst) and "frustration" would not have appeared if the conventional methods of analysing the responses had been used.

Book Reviews

Behaviour of the Great Tit (Parus major) and some other related Species. By R. A. HINDE. Supplement III *Behaviour*, Leiden: E. J. BRILL. 1952. Pp. 201, 11 figs., 38 tables. 54s.

This massive study of the behaviour of the Great Tit is undoubtedly the most comprehensive work on a single species of bird published since the newer ideas about instinct, with which ethology is so largely concerned, came to be generally known amongst biologists. As such it is of very great importance; for birds combine elaborate instinctive behaviour with a high learning ability to an extent which is almost if not quite unique in the animal kingdom.

Dr. Hinde sets out in the first place to provide as complete an account as possible of the annual cycle of the species as observed over two years in Marley Wood, Wytham, Berks. (one of the preserves of the Oxford University Dept. of Zoological Field Studies). This was followed by further observations and experiment on captive birds made in the aviaries of the Ornithological Field Station of the Cambridge University Dept. of Zoology at Madingley, and the work also includes a good deal of information and some new observations on other species of *Parus*. It is thus a valuable compendium on the behaviour of the genus.

The first step in the study was to colour-ring and thus make individually recognisable all the Great Tits frequenting Marley Wood. That this objective was achieved is striking testimony to the thoroughness of the work. Without the whole population thus being made identifiable from the start a study such as this could hardly have been brought to a convincing conclusion.

It is of course quite impossible in the course of a review to mention more than a small proportion of the significant facts and conclusions that have emerged from this admirable study. And in any event this should be unnecessary for it is a work which every ethologist and every ornithologist seriously interested in the study of behaviour will find he needs at hand for reference: consequently only a few of the theoretically more interesting conclusions will be mentioned.

The first problem to be studied was the organisation of the winter flocks. These flocks show a moderate degree of integration and move irregularly about a limited area of the wood.

While actually feeding the birds merely drift; but there are also more fully integrated movements during which the birds stop feeding and move for some distance. During these movements the "twink" call brings the birds into the mood for flight while the flying away of one bird tends to release the flying of the others. Besides the factors which tend to hold the flock together there are also disruptive factors at work, the chief of these being aggressive behaviour. This "winter fighting" is mostly concerned with disputes over food; it takes a number of different forms the most important of which is the "supplanting attack" in which one bird flies at another and takes possession of its food. Besides this there are also threatening postures in which, after the bird has sleeked and depressed its plumage as the first inevitable reaction to threat or invasion from a neighbour, the raised wings and forwardly stretched head are often sufficiently intimidating to repel a rival without actual attack. Persistent skirmishing can only occur when the fighting and fleeing drives are in almost exact balance—a state of affairs which generally occurs on or near the territorial boundary. Within the territory the fighting drive will usually be dominant and will lead to a successful supplanting attack, while outside it the fleeing drive will take charge of the situation. When drives are nearly balanced displacement activities are much in evidence, displacement pecking being the chief of these. The "head-up" posture so characteristic of threat in the genus *Parus* is itself thought to be an inhibited fleeing movement ritualised and stereotyped as a highly elaborate display in connection with which a special colour pattern has been evolved to make the display more conspicuous. The work on winter fighting as a whole has undoubtedly strengthened the position of the theory of "individual distance" and there now seems little doubt that the keeping of individual distance and the winter fighting that takes place in the flocks is of selective value. A number of interesting experiments with mirrors are described and the whole section on winter fighting is linked with another equally careful and valuable chapter on the patterns of reproductive fighting. There is evidence that food-fighting and reproductive fighting are distinct in that they are released by different stimulus situations, depend on different internal drives and utilise different postures. Nevertheless they are related

in various ways and it is shown that an individual with a high reproductive fighting drive also has a high food-fighting drive and *vice versa*. This and numerous other lines of evidence support the general conclusion of Tinbergen that the casual factors underlying instinctive behaviour are organised in a number of *interlinked* hierarchical systems. The significance of aggressive behaviour in the break up of the winter flocks and in the process of pair formation is also followed out with a remarkable wealth of detail.

This general subject of fighting drives and their inter-relations has been reviewed at length because it is in many ways central to the whole organisation of social behaviour in the Tits and gives clues to much of their ecology. Yet there are many other chapters of almost equal interest and importance which can be listed by title only. Thus pair formation, territory, song, copulation and courtship-feeding, nest site choice, nest building, incubation, care of the young, reaction to predators and roosting all have chapters to themselves and the author has something new and interesting to say on each of these topics backed in each case by a mass of careful observation and experiment. In short the work is an example which students of other species and groups, both of birds and of other animals will be well advised to follow and to use as a model.

Social Behaviour in Animals. By N. TINBERGEN. London: Methuen. 1953. Pp. xii + 150, 8 Plates, 69 line illus. 12s. 6d.

No life process or structure can be fully understood by the analysis of its causation alone: its contribution to the maintenance of individual and species must also be studied. In nearly all branches of biology function and causation must be considered together. Although this is particularly important in animal behaviour studies, most writers in this field have concentrated either on causation or (more rarely) on function: few have comprehended both.

In Dr. Tinbergen's previous book, "The Study of Instinct," the emphasis was mainly on causation, and function was treated only briefly. Here the balance is redressed. Social behaviour is divided according to function into four main groups—mating, family life, group life, and fighting—and the early chapters review the manifold ways in which these types of social co-operation are achieved. This naturally

necessitates some preliminary investigation of the mechanisms underlying the behaviour: this is developed in a later chapter where the innate basis of social behaviour is discussed. Dr. Tinbergen's own observations of the Grayling Butterfly, the Three-spined Stickleback, and the Herring Gull naturally form an important part of the subject matter, but the conclusions are based on examples drawn from animals of many different groups.

Learning processes as well as innate mechanisms are of course important in intra-species relations, and their role is considered in a chapter on the formation of social organisations. The evolution of social behaviour is also discussed.

Dr. Tinbergen interprets the word "social" very widely. "The study of social behaviour is the study of co-operation between individuals. There may be two individuals involved, or more." Even fighting is regarded as social behaviour on the grounds that it involves relations between individuals and is of use to the species. In his discussion of inter-species relations, however, Dr. Tinbergen sometimes steps outside his own liberal interpretation of "social." Those structures of plants which serve to attract insects, and the procryptic colouration of animals, can hardly be regarded as "social." Yet these topics are certainly relevant to the rest of the book—it is the title of the book which is misleading.

The book is pleasantly free from technical terms and the discussion can easily be followed by non-professionals. Indeed a final chapter of "Hints for research in animal sociology" is included for the benefit of the amateur, who, Dr. Tinbergen maintains, can still make important contributions in this field. "Social Behaviour in Animals" can thus be recommended to the amateur as an introduction to the study of the subject; to the general zoologist because of the evolutionary problems raised by the adaptiveness of behaviour; and to the ethologist as emphasising the often-neglected functional aspect of his work. R.A.H.

How Animals Move. The Royal Institution Christmas Lectures, 1951. By JAMES GRAY. Cambridge University Press. 1953. Pp. xii + 114. 16s.

Although delivered to a juvenile audience, the lectures upon which this book is based were a model of clarity, and as an exposition of the fundamental principles involved they may be

read with advantage by a much wider circle. Their value as an introductory text would have been enhanced by the addition of selected references.

Ecological Animal Geography. By W. C. ALLEE & KARL P. SCHMIDT. Chapman & Hall. 1951. Pp. xiii + 715. 68s.

Those familiar with the first American edition of this work will know that it was based on the late Richard Hesse's *Tiergeographie auf oekologischer Grundlage*. The process adopted for that first edition, viz., the intermingling of translated with fresh material, has been developed still further in an attempt to bring the whole of this comprehensive work up to date. For some reason the first edition was never very widely adopted in Great Britain, although it appears to have been a standard American text of some importance. The additions that have been made are extensive, and it is to be hoped that the work will now find its rightful place on British bookshelves, and will come to be used more widely by students. There is no work of comparable scope and documentation in the English language.

Physiological Foundations of Neurology and Psychiatry. By ERNST GELLHORN. Minneapolis: University of Minnesota Press. 1953. Pp. xiii + 556. \$8.50.

Though written primarily for neurologists, psychiatrists and clinical psychologists this book contains in its twenty chapters a great deal of material of prime importance to the student of animal behaviour. Dr. Gellhorn, whose general position indicates clearly the influence of that great physiologist W. B. Cannon, believes firmly in the value of synthesis; and in this book he has gathered up and given perspective to a vast amount of recent experimental work on integrative neurophysiology. Among the topics discussed are: The unit analysis of nervous activity; the motor cortex, voluntary movements and reflex activity; experimental convulsions; the physiology and pathology of consciousness; the autonomic nervous system; the principles of neuro-endocrine action; the physiological basis of emotion; factors involved in conditioning, and homeostatic mechanisms.

Unlike many psychological and behavioural writers Dr. Gellhorn seldom argues in advance

of experimental support. There are 1,263 references in the bibliography, more than ten per cent of which refer to the work of the author and his collaborators. It is inevitable that specialists will disagree with one or other of his interpretations. For example, his views on the so-called 'plasticity' of the nervous system, on the problem of the functional significance of the motor cortex and the probable role of the 'suppressor areas' in nervous homeostasis already have powerful dissentients, and a large number of the footnotes are devoted to explaining away evidence that does not fit with his story. But Dr. Gellhorn performs a valuable service in throwing into clear relief the functional interaction of different nervous 'levels' lying between stimulus and response. He stresses the importance of recent work on the functioning of the brain stem reticular system and the hypothalamus. The former is viewed in particular relation to spinal sensory and motor mechanisms and to its activating influence on the cerebral cortex. The hypothalamus receives attention in regard to its integration of somatic, autonomic and endocrine activity. Dr. Gellhorn shows how together they may serve as a basis for explaining many hitherto puzzling features of behavioural phenomena.

The reader who is interested in finding a neural substratum for ethological concepts of a hierarchical organisation of instinctive behaviour will find the book of particular relevance, for it effectively disposes of outworn ideas of localised nervous 'centres.' The gap between our knowledge of the integrated working of the nervous system and our knowledge of instinctive activities is still very large, and it is perhaps permissible to note that the former information is chiefly drawn from investigations on a few mammalian species, in which ethological data are scanty or non-existent. Nevertheless no theory of behaviour which ignores nervous mechanism is likely to win general acceptance, and this book provides perhaps the best account currently available of the present potentialities of neurophysiology in this respect.

The book is written in a clear style without flourish, and is bountifully illustrated with diagrams and experimental records and protocols. The type and paper are of a very high standard and the value of the work is enhanced by the numerous cross references and an excellent index.

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OBJECTS.

The Association for the Study of Animal Behaviour is a scientific society, founded in 1936. Its aim is to promote and co-ordinate work in animal behaviour, the study of which is of interest or importance to a wide range of biologists, e.g., those engaged in psychology, physiology, zoology, animal husbandry and veterinary science.

Scientific meetings are held, often in conjunction with other societies, and the Association possesses a library from which members may borrow, and to which all members are asked to contribute copies of their publications. From 1936 to 1952 the Association published at irregular intervals the BULLETIN OF ANIMAL BEHAVIOUR. This has now been replaced by a regular quarterly publication, the BRITISH JOURNAL OF ANIMAL BEHAVIOUR, which contains original scientific papers and reviews.

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